THERMOREGULATION IN FOUR SPECIES OF NESTING HERONS

By

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Temperature regulation in Louisiana Herons, Little Blue Herons, Cattle Egrets and Snowy Egrets is compared to investigate any different thermal requirements of these birds during nesting. Louisiana Herons and adult Little Blue Herons have dark plumage; Snowy Egrets and Cattle Egrets are white or nearly white. Louisiana Herons nest consistently in the shade. The other three species nest without regard to solar input, hence may nest in the sun.

Metabolic rates of adults are compared. Louisiana Herons have a high M_b, the two white herons have a somewhat lower M_b than expected from their weight, and Little Blue Herons have a M_b only 2/3 that expected. The low M_b of Little Blue Herons is considered an adaptation to nesting in the sun with dark plumage in a hot environment. It is shown that low M_b is characteristic of dark birds that have been studied in such environments.

Temperature regulation at the nest is investigated with regard to incubating adults and nestlings. A stable egg temperature of 35°C appears to be independent of parental attentiveness at normal T_a.

Little Blue Herons spend much less time incubating when exposed to the sun than do white Cattle Egrets. This behavioral response is thought to be a consequence of their dark plumage. Nestling T_b is nearly 39°C for all species regardless of age, brood size, or T_a as a result of 1) both parental and nestling behavior, which is described, and 2) the ability of nestlings to dissipate heat by evaporative means. Cooling curves are used to determine the development of homeothermy which in these herons is a function of age, not weight. Short-term homeothermy is achieved by 13 days, although there is some indication that Louisiana Herons achieve homeothermy later than the other three species. Growth rates are compared and all are tentatively considered to fit the logistic equation, although the Cattle Egret nearly conforms to the Gompertz equation. Possible thermal reasons are considered for the dark skin color in all four species and the white plumage of young Little Blue Herons.

CHAPTER 1

INTRODUCTION

Herons (Ardeiformes, Ardeidae) are nonpasserine birds with a wide range of size and distribution. Many of them breed in Florida; among these are four small species all with relatively similar nesting habits. Three of these species are probably congeneric (*contra* AOU Checklist, 1957); the fourth is a recent Old World arrival.

The Louisiana Heron (*Egretta* [=*Hydranassa*] *tricolor*) is probably slightly larger than the other species. It has a bicolored pattern, being a dark gray dorsally and white ventrally. The Little Blue Heron (*Egretta* [= *Florida*] *caerulea*) is the darkest bird, having a slate blue body plumage and rust-colored head and neck as an adult. The Little Blue Heron is unique among these four herons in having a marked difference between adult and juvenal plumage. Immatures have a white plumage which toward the end of their first year gradually molts to the adult plumage. Snowy Egrets (*Egretta thula thula*) have a completely white plumage. The Old World Cattle Egret (*Bubulcus ibis*) probably arrived from Africa on the northeast coast of South America in the nineteeth century, was first seen in Florida in 1941, and only began breeding in Florida in 1953 (Palmer, 1962). The Cattle Egret is basically white with patches of buff color on the head, back, and breast during the breeding season.

The inclusion of Little Blue Herons and Louisiana Herons with Snowy Egrets in the genus *Egretta* has only recently been proposed

(Dickerman and Parkes, 1968, Parkes, pers. comm.). Dickerman and Parkes noted hybridization of Louisiana Herons with Little Blue Herons and with Snowy Egrets. They also cited a note by Sprunt (1954) of a hybrid from a Little Blue Heron and a Snowy Egret cross. Curry-Lindahl (1971) suggested a reclassification of the Ardeidae on the basis of behavior and ecology. He too suggested that Little Blue Herons, Louisiana Herons and Snowy Egrets all belonged in *Egretta*.

All four species of herons have mainly tropical to subtropical breeding distributions, although a larger subspecies of the Snowy Egret (*Egretta thula brewsteri*) nests in several of the western states of the United States (Bent, 1926; Palmer, 1962). The Cattle Egret has recently invaded temperate areas in North America (Palmer, 1962; Weber, 1975), Australia (Palmer, 1962), and southern Africa (Siegfried, 1966a). The Cattle Egret invasion of temperate zones has mostly occurred since 1920 and is apparently a response to increased pasture land (Siegfried, 1966a). The tropical/subtropical distributions alone of these intermediate-sized nonpasserines makes them an attractive subject for study: most nonpasserines studied are temperate species.

All four of these herons nest together in mixed species heronries throughout Florida and the rest of the Gulf coast states. In Florida they nest in Spring when solar insolation is most intense. Their different colors under strong solar radiation must affect their nesting patterns in some way, yet no one has looked at nesting in herons from a thermal viewpoint. In fact, relatively little is known about their thermoregulation at all. Benedict and Fox (1927) reported rates of metabolism for the Great Blue Heron (*Ardea herodias*) and the American Bittern (*Botaurus*

lentiginosus); Siegfried (1969) measured the existence metabolism for Cattle Egrets at one temperature which was below their thermoneutral zone; Bartholomew and Dawson (1954) did some preliminary work on thermoregulation in nestling Great Blue Herons; and Hudson *et al.* (1974) described the development of endothermy in nestling Cattle Egrets. No comprehensive study has been done integrating the thermal requirements of adult and nestling herons with their actual conditions in the field. This study attempts to explain the thermoregulation of herons in the context of nesting in a hot environment.

CHAPTER 2

METHODS AND MATERIALS

Study Areas

Little Blue Herons, Louisiana Herons, Snowy Egrets, and Cattle Egrets were studied from spring 1971 through 1975. Most of the field work was done on Biven's Arm, a lake in Gainesville, Alachua County, Florida. Some solar radiation measurements were made on Riomar Island in the Indian River, at Vero Beach, Indian River County, Florida.

Biven's Arm has been described by Carr (1942), Rudegeair (1975), and Nordlie (1976). It has about 65 hectares of open water (Nordlie, 1976) and is surrounded by pasture and swampy woodland. The current heronry has existed on the northeast side since the early 1960's and probably represents the same heronry described by Jenni (1969) at Lake Alice 1.5 miles northwest from 1958 to 1960 (Nordlie, pers. comm.). Jenni speculated that the Lake Alice heronry had originally come from Biven's Arm in 1948. In 1972 some of the herons from the northeast side of Biven's Arm built nests on a series of five small islands on the southwest side of the lake. The islands were numbered sequentially 1 through 5 starting at the north. By 1973 as many as 40 percent of the herons on Biven's Arm nested on the southwest side of the lake. The southwest islands were anchored, and only on their outskirts was the vegetation partly floating or else slightly submerged. Some, if not all, of the islands were at one time floating free in Biven's Arm, presumably having been torn by winds from another part of the shoreline. Aerial

maps from 1967 do not show them on the southwest shore of the lake. The northeast heronry, on the other hand, is not clearly separated from the shoreline. A swamp of partly submerged vegetation, narrow waterways, and floating islands spans the few hundred meters between pasture and open water. The heronry occupies that part of the swamp closest to the open water, rarely penetrating more than 75 meters from it.

The four species of herons studied on Biven's Arm nested primarily in red maple (*Acer rubrum*) and elder (*Sambucus simpsonii*) which they shared with Anhingas (*Anhinga anhinga*) and, in most years, White Ibis (*Eudocimus albus*). Some buttonbush (*Cephalanthus occidentalis*) was intermixed with the red maple and elder in 1971, but virtually all of it died that year, and it only began to reappear in 1974. Floating cut-grass (*Leersia hexandra*) was abundant at the margins of the heronries and also scattered throughout most of the northeast heronry along or in the waterways. Pennywort (*Hydrocotyle* spp.) existed in spots at the water's edge at the heronry sites. By 1973 and especially 1974, very large growths of water hyacinth (*Eichhornia crassipes*) covered the water surface adjacent to the heronries.

Several other avian species nested within the heronries: Green Herons (*Butorides virescens*), Common Gallinules (*Gallinula chloropus*); Purple Gallinules (*Porphyrula martinica*); and Least Bitterns (*Ixobrychus exilis*) whose numbers increased dramatically in 1975 perhaps due to the expansion of water hyacinths. A very few American Coots (*Fulica americana*) and Black-crowned Night Herons (*Nycticorax nycticorax*) were occasionally seen in the heronry, but without evidence of breeding, at least during the spring and early

summer. In 1974 and 1975, Double-crested Cormorants (*Phalacrocorax auritus*) and a very few Great Egrets (*Casmerodius albus*) roosted at the southwest heronry at night. Boat-tailed Grackles (*Cassidix major*) and Red-winged Blackbirds (*Agelaius phoeniceus*) nested on the fringes of the heronry and less often within the heronry.

The Biven's Arm heronries were somewhat insulated from mammalian predation by water. However, a raccoon (*Procyon lotor*) was sighted in a tree in the northeast heronry on April 15, 1972, emptying two Little Blue Heron nests. Another raccoon was seen on the southwest shore next to Island 2 on May 9, 1973. Crows (*Corvus* spp.) were often seen at the height of the breeding season. Owls were apparently active predators in the heronry: owl pellets were found with piles of white feathers on the southwest shore. Alligators (*Alligator mississippiensis*) presumably ate young herons that fell out of their nests and perhaps adults drinking water below their nests. No snakes were ever seen in the heronries. Possibly Black-crowned Night Herons are occasional predators (Rudegeair, 1975).

Riomar Island is a spoil island with a large heronry described by Maxwell and Kale (1977). It has large Australian Pine trees (*Casuarina equisetifolia*), but the rookery occupies only mangrove trees, primarily black mangrove (*Avicennia nitida*) and white mangrove (*Laguncularia racemosa*). Most of the birds nesting with the four species studied here are also ardeids, the major exception being Brown Pelicans (*Pelicanus occidentalis*) which make up 11 percent of the breeding birds (Maxwell and Kale, 1974). Predation on Riomar Island was by Fish Crows (*Corvus ossifragus*) and potentially rats (*Rattus rattus*) according to Maxwell and Kale (1977).

Field Techniques

Observations at Biven's Arm were made from a rowboat, a tower, or occasionally from shore (only for the southwest islands). A 15 foot high tower with a 4-foot square observation platform 12 feet high was attached to a raft 10 feet by 15 feet in size. The raft could be moved by poling with a 16-foot pole which was equipped with a "duck bill" at one end to allow bracing against the soft mud bottom of Biven's Arm. By shrouding the top of the tower with burlap a movable blind-on-stilts was effected. Observations were made using 7 x 50 binoculars.

Nests on Biven's Arm were approached in a rowboat or a canoe when it was necessary to tag them for identification, or to observe, measure, or manipulate their contents. Many of the waterways in the large northeast heronry of Biven's Arm were kept open by the activity of alligators. Other paths clogged with cut-grass had to be cut open and then frequently maintained. Nests on Miomar Island were reached by walking.

Solar measurements were made with a dome solarimeter (model no. 615 from Science Associates) which integrated over a wavelength range of 0.3 μ to 3.5 μ (ultraviolet to far infrared) and which had a sensitivity of 25.8 mV/Langley (1 Langley = 1 cal/cm^2). The solarimeter itself was mounted on a 5 foot aluminum pole bent at 75°. At the opposite end of the pole a small bubble compass was attached at 75° so that the bubble was centered when the solarimeter was horizontal. Measurements were taken only between 1000 and 1400

hours Eastern Standard Time, when the sun was highest in the sky. Measurements were made of nests at a variety of heights.

Several kinds of air temperatures were taken. Shade and sun temperatures were usually taken with a Yellow Springs Instrument (YSI) telethermometer having 1°C divisions and using a YSI Type 402 small animal probe. Occasionally, these temperatures were taken with a mercury thermometer having 1°C divisions. In either case, the wind was shielded from the device. Black body temperatures were measured using a thermometer whose bulb was painted with flat black paint and dipped in black soot before drying. The black bulb thermometer, which had 1°C divisions, was wind-shielded by a tube painted flat black and having a slot for exposure to the sun's rays. Black body readings were always achieved by holding the thermometer normal to the sun's radiation.

Body temperatures of nestlings were measured using a YSI probe Type 402. All body temperatures were cloacal and probe penetration depth was 1-3 cm depending on the size of the chick. Occasionally skin temperatures were taken using a YSI banjo probe Type 409. If a parent had to be disturbed from a nest in order to reach the nestlings, temperature could usually be measured within 5 minutes of adult departure.

Nestlings were usually weighed whenever possible to determine growth characteristics. The weight of small nestlings was taken with a 100 g capacity Pesola spring scale having 1 g divisions; the scale had an accuracy of $\pm$ 1 g. Larger nestlings were weighed on a 200 g capacity double beam balance with 0.1 g divisions. Weights greater

than 200 g could be measured by putting some handy object on the second pan of the scale.

Egg temperatures were monitored in the nest by placing a synthetic egg in the nest. The synthetic egg was made from a heron's egg shell filled with Dow-Corning medical Silastic 382 Elastomar (Calder, 1971). A thermocouple wire was implanted in the egg which was put in the nest with the natural eggs. The thermocouple lead was kept on a makeshift spool and could be unwound about 100 feet to connect to a portable thermocouple meter (Minimite by Thermo Electric). The parent could be watched safely from a distance while egg temperature was simultaneously monitored.

Because the chicks of all four species studied hatch asynchronously (see Chapter 5), size differences were indicative of relative ages. Thus, it was unnecessary to mark individual chicks. Nests were monitored almost daily after about the twentieth day of incubation to record hatching dates. Nestlings on their day of hatching were considered 0 days old.

Laboratory Techniques

Feather reflectances were measured on a Bausch and Lomb Spectronic 20 spectrophotometer using a color analyzer reflectance attachment. A block of magnesium carbonate was used as a white reflectance standard. Reflectance was measured in feathers of intact birds, which had been preserved in a freezer, over a 340 mμ-900 mμ range.

Cooling curves were used to determine the time when homeothermy was first established in the young of these species. One nestling

from a given nest would be removed and brought to the laboratory only 1.5 miles away. Usually the bird was returned to the nest the same day, often within 4 or 5 hours of its removal. On a few occasions, heavy rain or darkness prevented this, but the bird would then be returned shortly after dawn the following morning. A thermocouple whose junction was encased in latex was inserted cloacally 1.5-3 cm depending on the nestling's size, and the wire was taped to the pygostyle region. The thermocouple was connected to a Honeywell chart recorder via a thermocouple reference junction. The nestling was put into a chamber which was placed in a water bath at 40°C. When the nestling began sustained large amplitude gular flutter (body temperature usually was within one degree of 40°C), it was put in another chamber which had been kept in a 17°C water bath. Ambient temperature was monitored with a YSI probe Type 402 which was suspended in the chamber. Cooling was continued at least 60 min or until body temperature closely approximated ambient temperature.

Metabolism was measured in adult herons using a Beckman G-2 paramagnetic oxygen analyzer connected in open circuit (Depocas and Hart, 1957). Air flow of about 1400 cm/min was pulled through the chamber and measured by a Brooks precision rotameter calibrated with a 500 cc Brooks volume-meter after carbon dioxide and water were removed. Carbon dioxide was removed from the air with color indicator grade soda lime (8-14 mesh), and water was removed by color indicator regenerated silica gel (grade H, type IV, 6-16 mesh). Only about 200 cm/min was put into the analyzer. Temperature and barometric pressure were recorded, and oxygen consumption was calculated at STP. Body tempera-

tures of the herons were taken with a Schultheis thermometer inserted 3-5 cm into the cloaca, within about a minute of the final metabolic measurement. All the adult herons measured, except the Cattle Egret, were raised in captivity and weighed about 20 percent less than wild herons. A weight difference between wild and captive-reared birds has also been noted for the Redhead (*Aythya americana*) by Weller (1957).

Statistical Methods

A variety of statistical tests was used, but all measures of variance given in the body of this paper are standard errors of the means, unless otherwise noted.

CHAPTER 3

NEST SITES AND SOLAR RADIATION

The nest sites of herons have been investigated before, but usually with respect to height, vegetation type, or relative placement when in a mixed species heronry (*cf.* Bent, 1926 and Palmer, 1962). Because solar radiation at the nest had never been measured before this study, a confused picture of nest site selection in herons existed.

At Biven's Arm, where most of this study was done, the same general nesting pattern was seen every breeding season from 1972 through 1975. Louisiana Herons, which arrived first, tended to nest close to open water. Little Blue Herons, in those years when they were present in relatively abundant numbers, tended to aggregate in groups of three to six or more nests, somewhat away from open water. Cattle Egrets, which were the last to nest in large numbers, chose nest sites without any obvious reference to open water. Snowy Egrets also appeared catholic in their selection of nest sites, but too few nested at Biven's Arm to make a definitive statement. All four herons nested in red maple or elder, the two most common trees, from 1.5-3 m above the ground or water.

Unfortunately, the internal consistency at Biven's Arm from year to year sheds no light on the observed nesting habits of these herons elsewhere. For example, Bent (1926) found Little Blue Heron nests on the outskirts of willow islands, only 2-4 feet above the ground. On the other hand, Meanley (1955) noted that Little Blue Herons nests

were closer to land (farther from open water), mainly in buttonbush swamp, and averaged 8 feet above the ground. Palmer (1962) states that Little Blue Heron nests tend to be grouped apart in mixed species rookeries. Bent (1926) found Louisiana Herons nesting on the ground in one rookery and as high as 15 feet in another. He noted that these herons occupied the center portion of mixed species heronries. However, Palmer (1963) says Louisiana Herons may also group around the periphery of mixed species colonies. Bent (1926) discovered Snowy Egrets nesting in open areas on the interior parts of an island (away from open water) whereas Meanley (1955) found them next to open water in a lake colony. Palmer (1962) suggested that Snowy Egrets can nest over 30 feet above ground, although 5-10 feet was more common. The influence of insolation may not clarify this picture entirely, but it is an important step in this direction.

Solar radiation was measured at nests on Biven's Arm and Riomar Island. Table 1 shows the solar radiation incident at the nests of all four species of herons; an F test showed that there were significant differences among the herons ($P < 0.05$). Observations in the field suggested that Louisiana Herons nested selectively in the shade. The other herons appeared to nest without any real reference to insolation. The data in Table 1 corroborate this: Louisiana Heron nests receive the lowest mean solar radiation input. Furthermore, both the upper and lower limits of the Louisiana Heron's range of insolation are lower than those of the other three species. Nonetheless, there is a broad overlap in the ranges of solar input at the nests of all four species. In order to clearly show the difference between Louisiana Herons and the others,

Table 1. Solar radiation[a] on heron nests.

	Louisiana Heron	Snowy Egret	Cattle Egret	Little Blue Heron
Range	0.046 - 1.279	0.136 - 1.306	0.112 - 1.473	0.081 - 1.391
$\bar{x} \pm$ s.e.	0.505 $\pm$ 0.070	0.595 $\pm$ 0.155	0.761 $\pm$ 0.050	0.645 $\pm$ 0.064
N	33	10	84	51
% above 1.200[a]	6.1	20.0	27.4	19.6

[a]Measured in Langleys/min = cal/cm^2 - min.

the proportion of highly exposed nests is compared in Table 1. The value of 1.200 Langleys/min (= cal/cm^2·min) is chosen for strictly heuristic reasons as a cut-off in the sun-shade continuum. Nests receiving 1.200 Langleys or more are considered to be under intense insolation. Only 6 percent of the Louisiana Herons fall into this category, whereas at least 20 percent of all the other species do. An *a priori* comparison of solar radiation at nests between Louisiana Herons and all the other herons yielded an F value (Sokal and Rohlf, 1969) which was highly significant ($P << 0.01$).

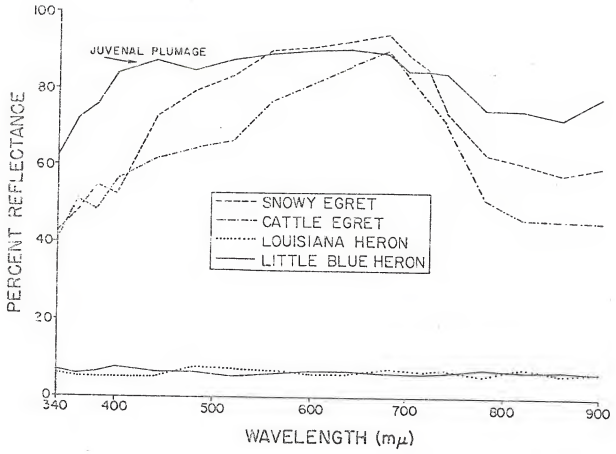
This difference in nest sites is important in Florida because all these herons nest in the spring when average insolation is greatest, and birds at exposed nests are subject to great thermal stress. By the time the summer rains begin, much of the nesting season is over. The eventual fate of most Louisiana Heron nests which were found in unshaded areas is unknown. However, one Louisiana Heron nest completely exposed to the sun was watched in 1974 and is described in Chapter 5. Bent (1926) implies, but does not actually state, that large numbers of Louisiana Herons may nest in the sun. The high energetic price that would be paid for this behavior by the adults is discussed in Chapter 4; the possible affect on nesting success is referred to in Chapter 5.

The orientation of nests in reference to an environmental parameter is well known. Piñon Jays (*Gymnorhinus cyanocephalus*) nest on the south side of trees in order to utilize the heat from solar radiation (Balda and Bateman, 1972). Desert Larks (*Ammomanes deserti deserti*) in the Negev desert build nests facing north and sheltered from the mid-day sun by rocks or vegetation (Orr, 1970). Calliope Hummingbirds (*Stellula calliope*) prevent nighttime heat loss by radiation to the heat sink of the

sky by building their nests just below a large branch (Calder, 1971). Roadrunners (*Geococcyx californian*) often build nests which are partly exposed to the sun but which have bands of shade to provide nestlings with a choice of thermal environments (Ohmart, 1973). Cactus Wrens (*Campylorhynchus brunneicapillus*) build closed nests whose entrances face away from the wind in the early cooler part of the breeding season but face them during the hot part of the season (Ricklefs and Hainsworth, 1969).

The effect of solar radiation on an animal can be described by the term $SoA(1 - r)$ [modified from Gates (1962)] where So is solar radiation, A is the animal's surface area, and r is its reflectance. Because the Louisiana Heron, Snowy Egret, Cattle Egret, and Little Blue Heron are all about the same size, A can be considered the same for all of them. So is also the same, because they all live together. So any differences in the effects of solar radiation on these birds will be a consequence of their reflectances. Figure 1 shows the percent reflectances for all these species as a function of wavelength as measured at the dorsal surface. The Little Blue Heron and Louisiana Heron are markedly darker than the Snowy Egret and Cattle Egret. The reflectance curves for the Louisiana Heron and Snowy Egret are probably slightly lower than normal because the specimens used had a duller plumage than is normally observed in the breeding season. However, it is doubtful that the curves would change very much with brighter plumage. Snowy Egrets and Cattle Egrets show a reflectance peak at the long visible wavelengths. Interestingly, the Little Blue Heron white juvenal plumage reflects more radiation over most wavelengths, including ultraviolet and near-infrared. Whether this is characteristic of juvenal plumages in the white Snowy Egret and Cattle Egret is unknown. Reflectance was not measured for the juvenal plumage of Louisiana Herons,

Figure 1. Feather reflectances in herons.


100
80
60
40
20
0
PERCENT REFLECTANCE
JUVENAL PLUMAGE
SNOWY EGRET
CATTLE EGRET
LOUISIANA HERON
LITTLE BLUE HERON
340
400
500
600
700
800
900
WAVELENGTH (mμ)

but, being dark, its reflectance curve is probably close to that of the adult.

The differences in reflectance mean that a Little Blue Heron or Louisiana Heron would reflect only about 6 percent of the solar radiation striking it, whereas the white birds would reflect 80-85 percent of the incident insolation. Feathers probably do not transmit much light. But whether the nonreflected radiation ($1 - r$) is absorbed by the feathers or transmitted directly to the skin, dark birds in direct sunlight must be under a considerably increased thermal load. Louisiana Herons have apparently adopted a strategy of nesting in the shade to cope with this problem. Little Blue Herons have apparently developed physiological and behavioral adaptations which allow it to nest in the sun. Their strategies will be discussed in Chapters 4 and 5.

CHAPTER 4

ADULT METABOLISM

The energetics of temperature regulation in endotherms can be expressed as

$$M = C(T_b - T_a) \quad (1)$$

where M is metabolism and represents the heat produced, C is thermal conductance, and T_b and T_a are body temperature and ambient temperature, respectively. The term $C(T_b - T_a)$ is an estimate of heat loss at low to moderate T_a when evaporative heat loss is low. As such, C should be considered "wet" thermal conductance (McNab, 1974) since it incorporates a small evaporative heat loss element. At higher T_a,

$$M = C'(T_b - T_a) + LE \quad (2)$$

where L is the latent heat of vaporization, E is the amount of water lost via evaporation, and C' is "true" thermal conductance. Because evaporative heat loss was not measured in this study and C is given as a minimum value at only low to moderate T_a, equation (1) will be used to discuss the energetics of thermoregulation. In an endotherm's thermal neutral zone, metabolism is basal (M_b) and equation (1) becomes

$$M_b = C(T_b - T_l) \quad (3)$$

where T_l is the lower limit of thermoneutrality.

An endotherm has then three variables to effect thermoregulation: M_b, C, and $(T_b - T_l)$. Any two of these factors can be modified, thus setting the third. Usually endotherms modify M_b and C (McNab, 1966a,

1970), thus determining $(T_b - T_\ell)$, the zone of thermoneutrality. A consideration of the determination of $(T_b - T_\ell)$ will follow later.

Both metabolism and conductance are weight-dependent functions. Lasiewski and Dawson (1967) showed M_b of nonpasserines to have the following relationship

$$M_b = 78.3W^{+0.723} \tag{4}$$

where M_b is in kcal/day and W is weight in kg. The form of equation (4) can be modified (McNab, 1974) to

$$M_b/W = 4.6W^{-0.28} \tag{5}$$

where M_b/W is in $cc0_2/g \cdot hr$, assuming 4.8 $cal/cc0_2$ (Brody, 1945), and W is in g. Conductance in birds is related to weight (Lasiewski *et al.*, 1967) as

$$C/W = 0.85W^{-0.51} \tag{6}$$

where C/W is in $cc0_2/g \cdot hr°C$.

Figures 2-5 show the metabolism of Louisiana Herons, Snowy Egrets, Cattle Egrets, and Little Blue Herons, respectively, as a function of ambient temperature. Minimum conductance is shown extrapolated through T_b at $M = 0$. Table 2 summarizes these results. Table 3 compares the observed basal metabolism and minimum conductance with that expected based on equations (5) and (6) respectively.

Metabolism

Resting metabolism was measured during daylight hours for adults of all four species of herons. Daytime metabolic measurements are a better estimate of heron energetics in the field when the birds experience thermal stress. A few nighttime measurements of metabolism

Figure 2. Louisiana Heron metabolism.

RATE OF METABOLISM (ccO2/g·hr)
2.0
1.0
5
10
15
20
25
30
35
40
Ta (°C)
--o-- LOUISIANA HERON 2
—x— LOUISIANA HERON 3
Tb (°C)
43
41
39

Figure 3. Snowy Egret metabolism.

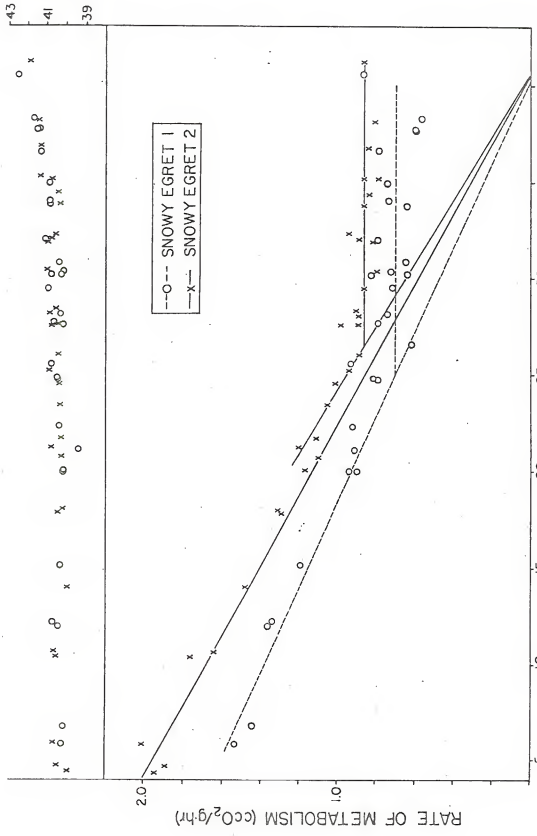

RATE OF METABOLISM (ccO2/g·hr)
2.0
1.0
5
10
15
20
25
30
35
40
Ta (°C)
43
41
39
Tb (°C)
--O-- SNOWY EGRET 1
—x— SNOWY EGRET 2

Figure 4. Cattle Egret metabolism.

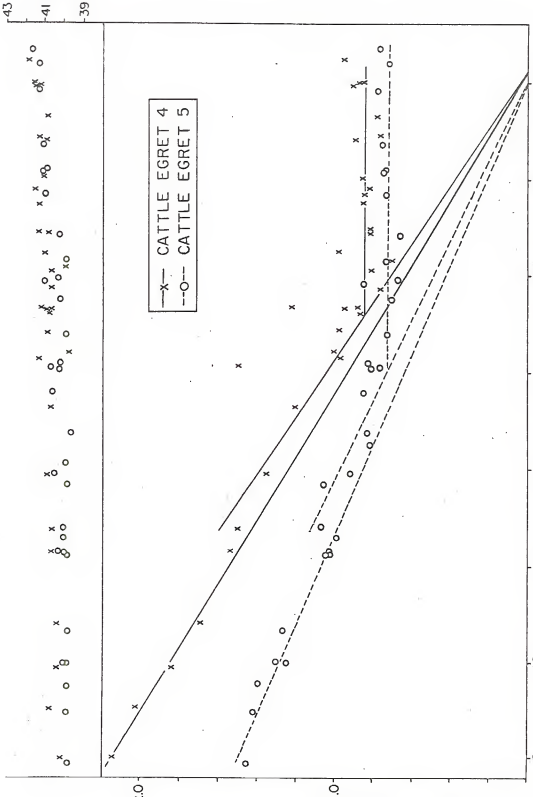

RATE OF METABOLISM (cc O2/g·hr)
2.0
1.0
5
10
15
20
25
30
35
40
Ta (°C)
43
41
39
Tb (°C)
—x— CATTLE EGRET 4
--o-- CATTLE EGRET 5

Figure 5. Little Blue Heron metabolism.

RATE OF METABOLISM (ccO2/g·hr)
2.0
1.0
5
10
15
20
25
30
35
40
Ta (°C)
Tb (°C)
43
41
39
--o-- LITTLE BLUE HERON 1
—x— LITTLE BLUE HERON 2

Table 2. Metabolic relationships in four species of herons.

Animal[a]	W[b]	M_b/W[c]	C/W[d]	T_b[e]	T_ℓ[f]
LOU 2	383.31 ± 2.59	0.951 ± 0.012	0.0579 ± 0.0012	40.4 ± 0.1	25.8
LOU 3	276.50 ± 5.75	1.033 ± 0.014	0.0615 ± 0.0025	39.7 ± 0.1	-- [g]
SE 1	333.73 ± 0.61	0.700 ± 0.020	0.0450 ± 0.0018	40.2 ± 0.1	26.5
SE 2	294.23 ± 1.51	0.869 ± 0.012	0.0549 ± 0.0019	40.4 ± 0.1	26.0
CE 4	271.67 ± 3.09	0.850 ± 0.015	0.0574 ± 0.0020	40.6 ± 0.1	28.0
SE 5	326.79 ± 1.04	0.745 ± 0.014	0.0427 ± 0.0012	39.9 ± 0.1	25.2
LB 1	259.63 ± 1.88	0.571 ± 0.010	0.0448 ± 0.0025	40.0 ± 0.1	27.8
LB 2	281.06 ± 1.57	0.670 ± 0.025	0.0475 ± 0.0028	40.4 ± 0.1	27.2

[a] LOU = Louisiana Heron, SE = Snowy Egret, CE = Cattle Egret, LB = Little Blue Heron

[b] weight in g

[c] basal metabolism in $cc O_2/g \cdot hr$

[d] minimum thermal conductance in $cc O_2/g \cdot hr °C \pm s_b$ (Sokal and Rohlf, 1969)

[e] body temperature in °C, where $T_a \leq T_\ell$

[f] lower limit of thermoneutrality in °C

[g] not enough data to determine T_ℓ

Table 3. Energetics of herons.[a]

Species	W	M_b/W	M_b%[b]	C/W	C%[c]	M_b/C	$(M_b/C)_e$[d]	F[e]	T_b	T_ℓ
Louisiana Heron	309.9	0.992	107	0.0590	129	16.8	20.2	0.83	40.0	25.8[f]
Snowy Egret	314.0	0.784	85	0.0500	110	15.7	20.3	0.77	40.3	26.2
Cattle Egret	299.3	0.798	85.5	0.0500	107.5	16.0	20.1	0.80	40.3	26.6
Little Blue Heron	290.4	0.620	66	0.0462	98	13.4	19.9	0.67	40.2	27.5

[a]Based on 2 individuals of each species, except as noted. Symbols as in Table 2.

[b]Percent of expected $M_b = 4.6W^{-0.28}$ (McNab, 1974, modified from Lasiewski and Dawson, 1967).

[c]Percent of expected $C = 0.85W^{-0.51}$ (Lasiewski *et al.*, 1967).

[d]Expected $M_b/C = \dfrac{4.6W^{-0.28}}{0.85W^{-0.51}} = 5.41W^{0.23}$.

[e]Ratio of observed M_b/C to expected M_b/C.

[f]Based on LOU 2 only.

in one Cattle Egret (CE1) showed conductance unchanged, but M_b was 24 percent lower than in the daytime. This is in close agreement with the estimate of Aschoff and Pohl (1970) that nighttime M_b is 25 percent lower than daytime M_b. There will be no discussion here of whether it is in fact proper to use the term "basal" metabolism in daytime measurements of diurnal birds. This distinction between daytime and nighttime measurements of metabolism is clouded because 1) the time of day is not always reported and 2) there is a tendency to avoid dealing with the distinction (*cf.* Lasiewski and Dawson, 1967). It should be noted, however, that the low values of M_b reported in this paper as would have been even lower had they been measured at night.

Table 3 shows that M_b for the smaller individual of a species pair is always significantly higher than for the larger individual ($P < 0.05$) using Student's t distribution (Simpson *et al.*, 1960). This should be expected from the weight relationship in equation (5).

Table 3 also shows that the Louisiana Herons were the only species whose M_b exceeded that predicted by equation (5) ($\bar{x}$ = 107 percent of expected). Both Louisiana Herons seemed more active or "tense" in the metabolic chamber than any of the other birds. Thus, it is possible that observed metabolism is a slight overestimate. Nevertheless, this species still appears to have the highest M_b. Louisiana Herons, which almost always nest in the shade, can be compared to the three other species which nest without reference to the sun. The average Snowy Egret M_b was 85 percent of expected. Although the range was large (77 and 93 percent), the average was quite close to the 85.5 percent average of the Cattle Egrets (whose range was small). Both of these

species are white or nearly white. Little Blue Herons had an average M_b of 66 percent of expected and have dark plumage. A few measurements on a yearling Little Blue Heron with white plumage were equally low.

It is unlikely that differences in M_b are phylogenetic; all the species except the Cattle Egret are congeneric. Furthermore, as discussed earlier, all have similar distributions. The differences in M_b may be directly attributable to thermal adaptations. Louisiana Herons, by nesting in the shade encounter low solar heat loads. Snowy Egrets and Cattle Egrets may nest in the sun but reflect a substantial amount of the sun's visible radiation. What extra heat load they bear is at least partly compensated for by a lower M_b. The most interesting case is the Little Blue Heron. This species may nest in the sun and, being dark, increase its thermal load. This increased thermal load at $T_a > T_{\ell}$ (most of the day and most days of the nesting season) probably reverses the thermal gradient from skin surface to feather surface, so that net heat flow is into the body (Lustick *et al.*, 1970). The greatly reduced M_b in Little Blue Herons is probably an adaptation to nesting in an environment with high insolation. This is not in itself unique and has been reported for Poor-wills (*Phalaenoptilus nuttalli*) by Bartholomew *et al.* (1962).

The interrelationship between dark color and metabolism has been investigated before, but generally in cooler environments. It can be summarized as follows: 1) birds dyed black (Hamilton and Heppner, 1967) and dark birds (Lustick, 1969) show a 23-26 percent reduction in the rate of metabolism when they are exposed to (artificial) solar radiation at temperatures below thermoneutrality.

2) This metabolic economy results from a decrease in the thermal gradient from the skin surface to the feather surface, thus lowering conductance (first suggested by Cowles, 1967; demonstrated by Lustick, 1969; Heppner, 1970; and Lustick *et al.*, 1970). 3) This reduction in conductance may result in a lowered T_{ℓ} and probably a lowered upper limit of thermoneutrality (Lustick, 1969). 4) All of this depends on an increased absorption of energy in the visible (Lustick, 1969; and Heppner, 1970) and perhaps near infrared spectrum (Lustick, 1969) by dark as opposed to white feathers. 5) It is suggested that dark birds stay out of the direct sunlight at $T_a > T_{\ell}$ (Lustick *et al.*, 1970) due to the earlier mentioned reversed thermal gradient between skin and feathers to which they would be subjected.

This last point is of particular interest because Little Blue Herons often nest in the sun at ambient temperatures well above their lower limit of thermoneutrality. It is not unusual for T_a to exceed 35°C in the field, whereas T_{ℓ} is 27.5°C (see Figure 5). Furthermore, incident solar radiation can easily exceed 0.9 cal/cm^2·min (Lustick, 1969) or even 1.23 cal/cm^2·min (Heppner, 1970). Solar radiation measured at nests (including those of Little Blue Herons) often exceeded 1.30 cal/cm^2·min. On May 26, 1973, a maximum of 1.43 cal/cm^2·min was recorded at 1315 hours on Biven's Arm.

Very few birds having dark feathers or skin and inhabiting hot environments have been investigated. Two of those may have been hypothermic and may have absorbed the sun's radiation to raise T_b. Heath (1962) and Ohmart and Lasiewski (1971) suggested this for Turkey Vultures (*Cathartes aura*) and Roadrunners (*Geococcyx californianus*) respectively. Road-

runners do not have dark plumage, but their feathers may be erected to expose their dark skin when basking. Ohmart and Lasiewski showed that although solar radiation was used to raise T_b in hypothermic Roadrunners, it was used to lower T_ℓ by reducing conductance in normothermic birds (much as in the birds studied by Hamilton and Heppner and by Lustick). By comparison, Little Blue Herons were never observed to bask in the sun (that is no special basking posture or orientation was noted), and there is no indication of hypothermia in this species.

Table 4 shows metabolic rate as a function of the expected rate from equation (5) for several dark nonpasserines which live in warm, mostly tropical climates; included is the Roadrunner which utilizes its dark skin for basking. If the data of Ohmart and Lasiewski (1971) are more accurate than those of Calder and Schmidt-Nielsen (1967) a low M_b is invariably correlated in dark birds with hot environments. McNab (1969, 1974) has noted a correlation between unpredictable food sources and low M_b. Both Turkey Vultures (Heath, 1962) and Roadrunners (Ohmart and Lasiewski, 1971; Ohmart, 1973) have unpredictable food supplies, as probably do Black Vultures; Little Blue Herons (Jenni, 1969; and others) and probably Magnificient Frigatebirds do not. However, Roadrunners (Ohmart, 1973), Magnificient Frigatebirds (pers. obs.), and Little Blue Herons all may nest in the sun. Vultures do not nest in the sun but may feed in full sun (pers. obs.). So while food habits may contribute to a low M_b in dark birds in hot environments ($T_a > T_\ell$). In this regard it may be noted that the temperate Brown-headed Cowbird, which can utilize sunlight to lower metabolic output at $T_a < T_\ell$ (Lustick, 1969), does not have a

Table 4. Comparative metabolism of some hot environment nonpasserines with dark plumage and/or skin.

Species	N	M_b%[a]	Source
Egretta (= Florida) caerula (Little Blue Heron)	2	66.0	Present study.
Geococcyx californianus (Roadrunner)	9(7)	97	Calder and Schmidt-Nielsen, 1976.
Geococcyx californianus	6	82.2	Ohmart and Lasiewski, 1971
Cathartes aura (Turkey Vulture)	2	70.4	Enger, 1957.
Coragyps atratus (Black Vulture)	2	79.6	Enger, 1957.
Fregata magnificens (Magnificient Frigatebird)	4	69.4	Enger, 1957.

[a]See Table 3.

low M_b although it is very dark. Lasiewski and Dawson (1967) found its M_b to be 99.3 percent of that expected for a passerine of its weight.

Metabolism and Insolation

In Turkey Vultures and Roadrunners, basking makes hypothermic birds normothermic. But Little Blue Herons, Louisiana Herons, Snowy Egrets, and Cattle Egrets all have the same high T_b of about 40°C. Insolation at high T_a can only make these birds hyperthermic; their T_b rises as they store heat. But because lethal T_b for most birds is around 45-46°C, there exists only a small margin for error in hyperthermic birds. The rate of change in body temperature ($\Delta T_b/\Delta t$) of a bird which is receiving solar radiation in a hot environment will be a function of internal heat production and external heat. The external heat load will be transmitted through the thermal gradient between feather surface and skin. This can be expressed as conduction

$$\frac{dQ}{dt} = KA\frac{dT}{dX} \tag{7}$$

where Q is heat; t is time; A is surface area; T is temperature; X is distance, and K is a constant. The distance between feather surface and skin may be considered constant, and equation (7) becomes

$$\frac{dQ}{dt} = C_1(T_f - T_s) \tag{8}$$

where T_f is feather surface temperature; T_s is skin temperature, and C_1 is a constant KA/X. Therefore, the rate of change in T_b can be expressed

$$\frac{\Delta T_b}{\Delta t} = \frac{M + C_1(T_f - T_s)}{KW} \tag{9}$$

where M is rate of metabolism, K is specific heat, and W is weight.

The net heat gain to the bird at high T_a is

$$C_1(T_f - T_s) = SoA(1 - r) - C_2(T_f - T_a) \tag{10}$$

where $C_1(T_f - T_s)$ is the conductive heat gain from the feathers, $SoA(1 - r)$ is the solar radiation striking the feathers, and $C_2(T_f - T_a)$ is the convective heat loss from the feathers. C_2 is a combined constant $(\frac{hc}{A})$ for convective heat loss (all other symbols are as previously defined). Equation (10) can be rearranged so that

$$T_f = \frac{SoA(1 - r) + C_1T_s + C_2T_a}{C_1 + C_2} \tag{11}$$

Substituting equation (11) into equation (9) for T_f,

$$\frac{\Delta T_b}{\Delta t} = \frac{M + C_1\left(\frac{SoA(1 - r) + C_1T_s + C_2T_a}{C_1 + C_2} - T_s\right)}{KW} \tag{12}$$

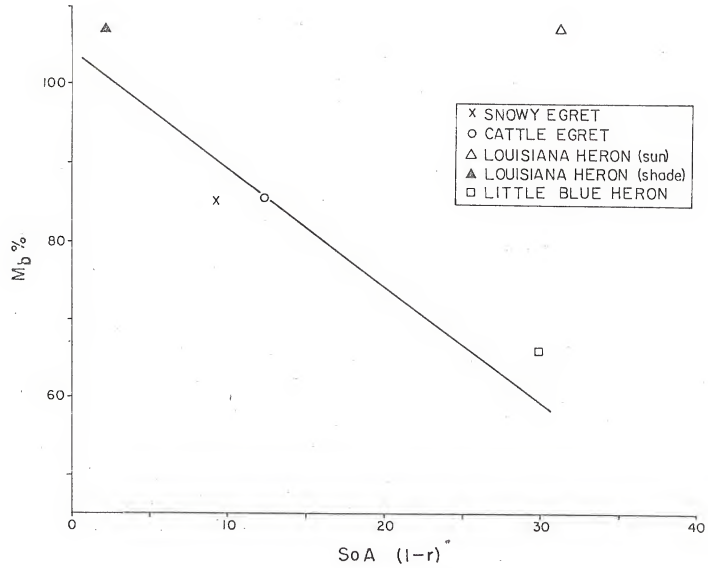
Assuming T_s and T_a to be constants, equation (12) simplifies to

$$\frac{\Delta T_b}{\Delta t} = \frac{M + K_1[SoA(1 - r)] + K_2}{KW} \tag{13}$$

where $K_1 = \frac{C_1}{C_1 + C_2}$ and $K_2 = \frac{C_1^2 T_s + C_1C_2T_a}{C_1 + C_2} - C_1T_s$.

It is now apparent that the rate of change of T_b is a function of both rate of metabolism and solar input. Figure 6 shows the relation between $\dot{T}_b$ expressed as a percent of that expected by weight (see Table 3) and solar input, $SoA(1 - r)$. $SoA(1 - r)$ was calculated using the

Figure 6. Metabolism vs. solar radiation in herons.


100
80
60
0
10
20
30
40
M_b %
SoA (1−r)"
X SNOWY EGRET
O CATTLE EGRET
△ LOUISIANA HERON (sun)
▲ LOUISIANA HERON (shade)
□ LITTLE BLUE HERON

average reflectance from Figure 1, $So = 1.43$ cal/cm^2·min, and $A = W^{0.67}/2$ (because rarely would solar radiation impinge on more than 50 percent of a bird's surface area). Figure 6 shows that Louisiana Herons in the sun have high % M_b and high $SoA(1 - r)$ due to their low r. They thus would heat rapidly, and consequently remain mostly in the shade. Snowy Egrets and Cattle Egrets have a slightly depressed % M_b but their $SoA(1 - r)$ is very small due to their high r. Little Blue Herons have the lowest % M_b which compensate for their high $SoA(1 - r)$ that a low r gives them. Little Blue Herons can take advantage of a low M_b when in the sun so that their rate of T_b increase is relatively slow.

Conductance

Table 2 summarizes the data provided in Figures 2-5 for minimum thermal conductance. Table 3 compares these minimum conductances with the conductances predicted by weight in equation (5). C is equal to or greater than expected in every case. There is a clear trend in these values similar to the data for M_b. Louisiana Herons have the highest C (129 percent) and nest in the shade. Snowy Egrets and Cattle Egrets which may nest in the sun but are white have intermediate values of 110 and 107.5 percent respectively. The dark, often sun-nesting Little Blue Herons show a C of 98 percent. Dawson and Hudson (1970) indicate that birds in hot environments tend to have high values of C for heat dissipation. Yarbrough (1971) cites data to that effect.

What then is the significance of a relatively low C? It is doubtful that these herons can use it to much advantage to insulate themselves

against the sun's radiation: C is still too high. A low C, however, may have an entirely different function. As a consequence of equation (3),

$$M_b/C = T_b - T_\ell \qquad (14)$$

That is, the zone of thermoneutrality is a function of M_b and C. A reduction in M_b would lower $(T_b - T_\ell)$ unless compensated by a lower C. Thus a lower C may be the means by which an endotherm maintains a relatively wide thermoneutral zone even while decreasing its heat production. This may explain the low C value of Little Blue Herons. Even so, its zone (13.4 $\pm$ 0.7°C) is significantly smaller ($P < 0.05$ using Student's t) than any of the other species (16.2 $\pm$ 0.7°C) when calculated as M_b/C. An analogous situation may be found in Poor-wills. Poor-wills nest in the sun and have a very low (49 percent) M_b (Bartholomew *et al.*, 1962). They also have a C of 94 percent. This C probably is not so important for its insulative properties as it is in guaranteeing a wider thermoneutral zone. For example, the thermoneutral zone of a Poor-will is 6.56°C as calculated by M_b/C. If the Poor-will's C had been 100 percent, M_b/C = 6.18°C. Higher C, though good for heat dissipation would narrow further this species' ability to cope with its environment.

Empirically determined $(T_b - T_\ell)$ in Little Blue Herons (12.8 $\pm$ 0.5°C) is not significantly different from that of the other herons (14.4 $\pm$ 0.4°C). This is due to the high T_ℓ (28.0°C) of CE 4. An estimate of the lower limit of thermoneutrality at minimum thermal conductance (T_L) is given in Table 6. Because the changes in C with decreasing

T_a are essentially behavioral (see below), (T_b - T_L) of Little Blue Herons (12.8 ± 0.5°C) is significantly lower than that of the other herons (15.9 ± 0.5°C) using Student's *t*-test ($P < 0.05$).

Determination of Thermal Conductance

Conductance is the coefficient of heat loss in the Newtonian model of equation (1). In an endotherm whose total response to T_a below T_ℓ is chemical regulation, C is the slope of the regression of metabolism, on decreasing T_a. In these cases C extrapolates to T_b in accordance with equation (1). This is rarely the case in birds, however. Most birds show a mixing of chemical and physical regulation at $T_a < T_\ell$. This manifests itself as a steadily decreasing C as T_a decreases (Schmidt-Nielsen, 1975: 323). In this case the regression of metabolism on T_a extrapolates to a figure in excess of T_b. The slope of this regression if presented as C will be an underestimate. Contrary to King (1964) this does not invalidate Newton's law of cooling as a model (Scholander *et al.*, 1950); it simply reaffirms that birds mix physical responses with chemical responses to low T_a. In these cases there may be a family of slopes which decrease as T_a decreases and which converge at T_b (*cf.* Figures 2-4). Minimum thermal conductance is that conductance which represents purely chemical responses to decreased T_a; where mixing of responses occurs, it is found at the lowest T_a values. This minimum conductance is the C of equation (1).

Although C cannot be equivalent to the slope of a line which does not extrapolate to T_b, it can be calculated in several ways. In this paper C was considered to be the lowest slope of the family of slopes

which converge at T_b. C has been calculated based on the metabolic response to the lowest T_a measured (Lasiewski *et al.*, 1970). Calder and Schmidt-Nielsen (1967) considered

$$C' = \frac{M - LE}{(T_b - T_a)\cdot S} \qquad (15)$$

where S is surface area. This is a form of equation (2). Here is true dry thermal conductance. Unfortunately, most of the literature is based on "wet" thermal conductance (*cf.* Lasiewski *et al.*, 1967). However, since T_a is normally low, LE should be fairly small and C' should be only slightly less than C. Using the data Calder and Schmidt-Nielsen (1967) present for the Roadrunner, I calculated the minimum slope C (extrapolated to T_b) as 0.0473 $cc O_2/g\cdot hr\cdot °C$ (100 percent of expected). This differs from the average low T_a C' of 1.30 $cal/m^2\cdot hr\cdot °C$ (= 0.042 $cc O_2/g\cdot hr\cdot °C$) by less than 12 percent.

A slightly more accurate calculation of C would involve using the same data points which produce minimum conductance in a slightly different way. Recognizing that the extrapolation to T_b involves an average T_b, each metabolic value can be regressed on its own T_b. A family of slopes, whose average is an estimate of C, results. Table 5 shows the difference between "minimum" conductance and "average" conductance; the former is a slope itself, the latter is an average of values determined by several slopes. In sever out of eight cases in Table 5, the average value gives a higher estimate of C. If these results can be generalized, all methods of calculating C differently than the last averaging method, tend to underestimate the parameter.

Table 5. Comparative measurements of conductance in four species of herons.

Animal	C_{min}[a]	C_{avg}	C_{avg}/C_{min}
LOU 2	0.0579	0.0575	0.993
LOU 3	0.0602	0.0616	1.023
SE 1	0.0450	0.0464	1.031
SE 2	0.0549	0.0566	1.031
CE 4	0.0574	0.0641	1.117
CE 5	0.0427	0.0431	1.009
LB 1	0.0448	0.0482	1.076
LB 2	0.0475	0.0553	1.164

[a] C_{min} = C/W in Table 2.

Body Temperature

It was stated earlier that once M_b and C were established ($T_b - T_\ell$) was set. This is simply a consequence of equation (3). ($T_b - T_\ell$) is of course itself not a single variable but is the difference between two variables, one of which may be selected for. T_b is usually higher for birds than mammals of the same weight. This is a consequence of a generally higher M_b and lower C in birds (McNab, 1966b and 1970). T_b and T_ℓ are related to each other and body weight. This can be expressed as

$$T_b = 5.41FW^{0.23} + T_\ell \qquad (16)$$

where $5.41W^{0.23} = 4.6W^{-0.28}/0.85W^{-0.51}$ the expected ratio (M_b/C) for birds (Lasiewski and Dawson, 1967 and Lasiewski *et al.*, 1967) and F is the relative ratio between observed and expected M_b/C [equation (16) is modified from McNab, 1970]. Table 6 shows that T_b is close to that predicted by equation (16). T_b measured for Cattle Egrets in this study (40.6°C) agrees well with the T_b for wild and captive Cattle Egrets (40.46°C) reported by Siegfried (1968). Wetmore (1921) reported Snowy Egret T_b at about 40°C which corresponds closely to the 40.6°C reported here. Table 6 also shows that the differences in ($T_b - T_\ell$) between Little Blue Herons and the other three species mentioned earlier is due to differences in T_ℓ. When T_b of Little Blue Herons (40.3 ± 0.2°C) is compared to an average T_b for Louisiana Herons, Snowy Egrets and Cattle Egrets (40.5 ± 0.2°C), there is no significant difference nor is there when comparing T_ℓ. But T_L for Little Blue Herons is significantly higher than the other species (27.5 ± 0.3°C vs. 24.7 ± 0.5°C, $P < 0.05$) using a

Table 6. Comparative energetics of herons.[a]

Animal	M_b/C	$(M_b/C)_e$	F	T_b[b]	T_ℓ	$(T_b - T_\ell)$	T_L[c]	$(T_b - T_L)$	$(T_b)_e$[d]
LOU 2	16.425	20.721	0.793	40.7	25.8	14.9	23.9	16.8	42.3
LOU 3	17.159	19.715	0.870	40.9	--	--	--	--	--
SE 1	15.556	20.586	0.756	40.6	26.5	14.1	25.0	15.6	42.1
SE 2	15.829	19.998	0.792	40.7	26.0	14.7	25.0	15.7	41.8
CE 4	14.808	19.641	0.754	40.9	28.0	12.9	26.4	14.5	41.3
CE 5	17.447	20.487	0.852	40.4	25.2	15.2	23.3	17.1	42.6
LB 1	12.746	20.096	0.634	40.1	27.8	12.3	27.8	12.3	40.5
LB 2	14.105	19.789	0.713	40.5	27.2	13.3	27.2	13.3	41.3

[a] Symbols as in Tables 2 and 3 unless otherwise noted.

[b] Body temperatures at all T_a unless above thermoneutrality.

[c] Estimated at minimum thermal conductance.

[d] Estimated $T_b = 5.41FW^{0.23} + T_\ell$ (modified from McNab, 1970).

t-test. It appears that a high T_b is being selected for. In the equation $M_b = C(T_b - T_\ell)$, T_ℓ is the dependent variable. Little Blue Herons then show a different temperature response to hot environments than do Turkey Vultures (Heath, 1962) and Roadrunners (Ohmart and Lasiewski, 1971) both of which bask to compensate for hypothermia. Little Blue Herons, which are normothermic and do not bask, adjust T_ℓ. As stated earlier, the differences probably are due to the unpredictable food supply of Turkey Vultures and Roadrunners.

Energetic Implications

Yarbrough (1971) has argued that tropical or desert (*i.e.*, warm habitat) birds show a low F value [his $(M_b/C)_r$] and have a low $(T_b - T_\ell)$. The F values in Table 6 are in fact low with the Little Blue Herons ($F = 0.674 \pm 0.040$) being significantly lower than the pooled F of the other species (0.803 ± 0.034) using a t-test ($P < 0.05$). Table 6 also shows that $(T_b - T_\ell)$ is lower than the expected ratio $(M_b/C)_e$ would predict.

Siegfried (1969) measured "aviary-existence energy level" as 100 kcal/day for a 383 g Cattle Egret at 16-19°C. This is equivalent to 2.27 $cc O_2/g \cdot hr$ where average $T_a = 17.5$°C. Siegfried showed that this was about triple standard metabolism (M_b); actually it is 2.61 times M_b [calculated as predicted by Lasiewski and Dawson (1967) in equation (5) above]. Figure 4 shows that a Cattle Egret uses an average of 1.21 $cc O_2/g \cdot hr$ at 17.5°C. Hence aviary existence energy is 1.88 times resting metabolism at the 16-19°C range. This value is a more useful estimate than Siegfried's. If one could generalize to all ambient

temperatures, existence energy is about double resting rates, a figure which could be used as a starting point for predicting energy budgets for these birds.

CHAPTER 5

THERMOREGULATION AT THE NEST

If it is true that the relatively low metabolism of some adult herons is, at least in part, a consequence of nesting in areas exposed to high solar radiation, then behavioral modifications might also be expected. The preference among Louisiana Herons for shaded nest sites is one such modification. A field study of the nesting habits of Louisiana Herons, Little Blue Herons, Cattle Egrets, and Snowy Egrets with respect to thermoregulation revealed several behavioral differences among these birds.

All four of these species build relatively open stick nests which are unlined. They all lay eggs which are essentially indistinguishable in color (light blue) and size. Varying clutch size in these species has been reported in different years and localities ranging from 3 to 7 eggs (Bent, 1926; Howell, 1932; Meanley, 1955; Teal, 1965; Dusi, 1966; Blaker, 1969; Hopkins and Murton, 1969; Dusi and Dusi, 1970; Shanholtzer *et al.*, 1970; Weber, 1975), but all showed a clutch size of about 3 in the Biven's Arm study area (Table 7). The young of all four species hatch asynchronously after similar incubation periods of 23 $\pm$ 2 days (Palmer, 1962; Weber, 1975).

One conspicuous difference, however, is in nestling plumage coloration. The dark Little Blue Heron has young with white plumage as do the white Snowy Egret and Cattle Egret. The relatively dark Louisiana Heron has young with a dark brown plumage. Paradoxically,

Table 7. 1974 clutch size at Biven's Arm

	Louisiana Heron	Little Blue Heron	Snowy Egret	Cattle Egret
$\bar{x} \pm$ s.e.	3.3 ± 0.1	2.7 ± 0.2	3.0 ± 0.4	3.0 ± 0.1
N	17	7	4	26

all four species hatch with only sparse down and heavily pigmented dark blue (occasionally dark green in Cattle Egrets) skin. These differences plus those already discussed in the adults are mainly responsible for the differences in thermoregulatory behavior at the nest.

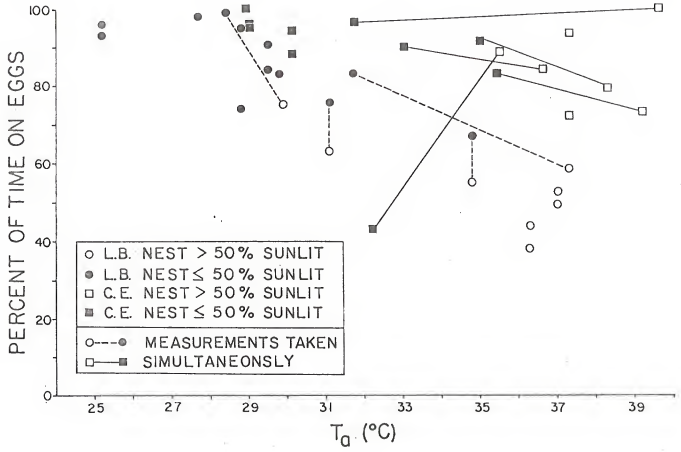
Incubation

Attentiveness, or time spent on or at the nest is one of the most important parameters of incubation. Unfortunately, this term connotes different behaviors in different kinds of incubators. "Attentive period" for single-sex intermittent incubators means the time spent at the nest, whether on the eggs or not, as opposed to "inattentive period" spent in foraging, maintenance activities and social interactions. This is the usage of White and Kinney (1974) even though they define attentive period as the "time spent on the nest per unit time" (emphasis added). For bisexual incubators where both parents alternate at the nest, the situation is different: one parent is always present at the nest. The attentive period for these birds is best considered as the time spent on the nest, that is actually sitting on eggs. Then inattentive time becomes the time not actually on the eggs; it is spent the same way as in single-sex intermittent incubators except for foraging. This distinction would follow Skutch (1962) although not using his "session/recess" terms.

Attentiveness was examined for Little Blue Herons and Cattle Egrets to assess the effect of plumage color on the incubating adults. The dark Little Blue Herons and the nearly all white Cattle Egrets were selected as representatives of the heron color spectrum. Nests in the shade were compared to nests in the sun; the latter were inspected on sunny and

cloudy days. To best handle the data, an arbitrary decision was made to consider all nests more than 50 percent in the sun as "sunny" and nests with 50 percent or less sun (due to clouds or natural shade) as "shady." A total of 35.9 hours were spent watching seven Little Blue Heron nests and four Cattle Egret nests for 60 min or longer periods at randomly selected times between 1030 and 1730 hours under a variety of environmental conditions. Attentiveness (percent time on the eggs) was considered as a function of ambient temperature. The results are presented in Figure 7. As T_a increased, attentiveness tended to decrease for both species. Shady nests were about the same for both, although Cattle Egrets appeared to be slightly more attentive. At sunny nests, however, although attentiveness continued to fall with increasing T_a, Little Blue Herons spent noticeably less time on the nest than did Cattle Egrets. Lines connecting two points in Figure 7 represent pairs of measurements made simultaneously. Here environmental conditions such as wind, humidity, and cloud cover were identical; only the degree of cover from the sun varied. All pairs involved one sunny nest and one shady nest. Four of five lines connecting pairs of Cattle Egret nests are mostly horizontal reflecting the expected difference in T_a between a sunny and shady nest. However, the lines connecting pairs of Little Blue Heron nests have a considerable vertical component as well. Little Blue Herons were behaving in the sun as if T_a were even higher than it was. This must be a consequence of dark plumage increasing the thermal load on a bird, probably by reversing its skin to feather surface thermal gradient (see Chapter 4). The general relationship of decreasing attentiveness with increasing T_a has been noted before for Cattle Egrets (Lancaster, 1970), White Ibis

Figure 7. Attentive time comparison between Little Blue Herons and Cattle Egrets in sun and shade.


PERCENT OF TIME ON EGGS
100
80
60
40
20
0
25
27
29
31
33
35
37
39
T_a (°C)
L.B. NEST > 50% SUNLIT
L.B. NEST ≤ 50% SUNLIT
C.E. NEST > 50% SUNLIT
C.E. NEST ≤ 50% SUNLIT
MEASUREMENTS TAKEN
SIMULTANEONSLY

(Rudegeair, 1975), and for single-sex incubators as diverse as Mallards (Caldwell and Cornwell, 1975) and small passerines (White and Kinney, 1974). This relationship is probably directly related to incubation. As T_a approaches egg temperature, the gradient between them is reduced, and longer periods of inattentiveness can be tolerated without risk of a critical drop in egg temperature. For Little Blue Herons on shady nests and all Cattle Egrets, time spent off the eggs was used, in decreasing order of occurrence, to preen, adjust nest material or eggs, engage in aggressive interactions with neighbors or interlopers, and gather new nest material. All these activities but the last, which was very rare, occur at or very close to the nest site. The most common behavior of Little Blue Herons on sunny nests when off the eggs was to adopt a "shading" posture as described by Bartholomew (1966). Here the bird's back is to the sun, wings are drooped, and gular flutter is common. There is no reason, however, to believe that these birds are trying to prevent their eggs from overheating; otherwise Cattle Egrets at the same T_a and on sunny nests would show this behavior. More likely, these Little Blue Herons are trying to prevent themselves from overheating by posturally increasing their convective heat loss. Nevertheless, by effecting this posture while standing over the nest, solar overheating of the eggs is prevented. On a few occasions though, a Little Blue Heron would walk off a sunlit nest and stand for a few minutes in the shade. Postural responses to thermal stress in incubating adults have been reported before by Howell and Bartholomew (1962) for Sooty Terns (*Sterna fuscata*) and by Bartholomew (1966) for Masked Boobies (*Sula dactylatra*). The thermal stress resulting from insolation on dark plumage was also

evidence by the fact that Little Blue Heron adults in the sun always showed gular flutter (a mechanism of evaporative heat loss) at lower T_a than Cattle Egrets, Snowy Egrets, or White Ibises (pers. obs.). Furthermore, Cattle Egrets on sunny nests showed the same postural "shading" as Little Blue Herons, but only at more elevated levels of T_a.

Two Louisiana Heron nests were observed on two occasions. One adult was on the eggs 96.8 percent of the time where the nest was shaded from a cloudless sky at T_a = 28°C. The other adult was on the eggs 100 percent of the time on a very cloudy day when T_a = 28°C also. These observations agreed with my general impression that Louisiana Herons, which usually nest in the shade, are very attentive. However, no Louisiana Herons that nested in the sun were observed (almost none existed), and there are insufficient data to draw general conclusions about attentive time for this species. Snowy Egrets were not observed at all in this regard.

On three occasions, it rained during observations of Little Blue Herons and Cattle Egrets. Attentive time increased to 100 percent each time. This increase in attentiveness during rain is also reported by Caldwell and Cornwell (1975) and Rudegeair (1975).

Egg temperatures were monitored with a synthetic egg. In the morning, egg temperatures were usually below 34°C and rarely fell as low as 20°C. Egg temperatures stabilized by around noon and remained around 35°C regardless of attentiveness by the adult (see Table 8). The stabilized egg temperatures of these herons are relatively low compared to those of most birds studied (Drent, 1973). Lundy (1969) found in chickens that egg temperatures below 35°C reduced hatching success. The egg tempera-

Table 8. Heron egg temperatures.[a,b]

		LB-2	LOU 9	SE 3	CE 0	CE 108
Pre-stabilization	$\bar{x} \pm$ s.e.	31.9 ± 0.4	--	31.7 ± 0.4	31.1 ± 0.2	32.4 ± 0.4
	N	9	0	9	8	10
Post-stabilization	$\bar{x}$ + s.e.	34.9 + 0.2	34.9 + 0.4	35.2 + 0.3	34.7 ± 0.2	34.4 ± 0.3
	N	17	11	15	16	23
Number of eggs in clutch before synthetic egg added		2	2	3	2	1

[a]Symbols as in Table 2; numbers refer to nest.

[b]Measurements in °C.

ture of the Herring Gull (*Larus argentatus*) which like ardeids has bi-sexual incubation, is about 38°C (Drent, 1970).

These apparently low egg temperatures may be the result of using a synthetic egg. The thermocouple from the egg left through the bottom of the nest. Perhaps because it could not be turned or otherwise moved, the synthetic egg was usually pushed to the bottom of the nest. At least once the egg was pushed nearly completely through the bottom of the nest. An egg pushed down in the nest would not only be farther from the incubating adult and any incoming solar radiation, but also it would be subject to updrafts and winds through the open weave stick nest. This would be exaggerated in the cool morning when the birds are moving off the eggs occasionally. Egg temperature can be adjusted by the tightness of sit (White and Kinney, 1974). Tightness of sit can be expected to increase at night when the adult settles down to sleep. One nest, CE 108, was monitored one night from 2300 hours to 0500 hours the following morning. During this period, the adult never got off the eggs and egg temperature stayed within a degree of 35°C. This tends to confirm the hypothesis that the morning egg temperatures were low as a result of the synthetic egg being pushed to the bottom of the nest and in the absence of good tightness of sit.

There is no evidence of the presence or absence of incubation patches in Ardeidae in any of the literature searched (*e.g.*, Jones, 1971).

Behavioral Temperature Regulation

Chicks of all four heron species usually hatch asynchronously. Blaker (1969) showed that asynchronous hatching in Cattle Egrets had

a marked effect in nest siblings' competition for food. Rarely was the third (or fourth) nestling able to compete with its older siblings, and if it survived, it showed a slower rate of growth than the first two (Blaker, 1969; Siegfried, 1972). Ohmart (1973) demonstrated that asynchronous hatching in Roadrunners allowed regulation of the brood size in relation to food supply.

After hatching, attentiveness should be defined as time spent at or nearby the nest. The parents continuously attend the young after hatching until the eldest is at least one week old. Four Louisiana Heron nests, 14 Cattle Egret nests, and three Little Blue Heron nests were watched at random hours every day after their eggs hatched for evidence of parental absence. The first parental absence from the nests was observed when the oldest nestling was 12.6 $\pm$ 0.7 days (range 8-19 days), with no apparent differences among the three species. Most of the nests had two nestlings, although only one nestling occurred in one nest of each species. Because observations were not continuous, 12.6 days is probably an overestimate of the eldest nestling's age at first parental absence. Weber (1975) noted continuous attentiveness for about 14 days in Cattle Egrets whereas Blaker (1969) noted that no nest is left "unguarded" before chicks are 10 days old. In three nests with twins, Blaker noted continuous adult presence for an average of 13 days, and in three singleton nests he noted continuous attentiveness for an average of 16.7 days. One Louisiana Heron nest is not calculated into the mean nestling age. Its only young was 23 days old at first parental absence; the significance of this nest will be discussed later. The first parental absence does not signify an end to the attentive period. On the contrary, the parents

may still spend a great deal of time at the nest, particularly in the middle of the day when T_a is maximum. Attentiveness does gradually diminish with time however.

During the period of attentiveness, the parents behave in such a way as to ameliorate the thermal environment. This behavior changes as the nestlings grow older. The adult usually broods the nestlings for about one week after hatching. At first this may serve the additional purpose of incubating any remaining eggs in the nest. But even after the last young is hatched, the adult will frequently brood its nestlings. This behavior, which shields nestlings from cool T_a or cooling breezes, was usually seen in the morning or evening hours. Nestlings as old as 5 or 6 days were often brooded in this way. Occasionally older chicks were similarly brooded; for example, a Snowy Egret (SE 3) parent lay on its 13-day-old nestling under a cloudy sky when T_a = 32°C or less on May 31, 1975. It is possible that this parental behavior was normal at night. On July 7, 1974, at 1600 hours an adult Cattle Egret (CE-106) brooded four young aged 4-7 days; another Cattle Egret (CE 109) was seen to gently lie down on the 12-day-old nestling which had been standing between its legs; a third Cattle Egret (unnumbered) stood hunched over with its large 18 day nestling between its legs.

No evidence of shivering was noted for any of the species as reported for Cattle Egrets by Blaker (1969) and Hudson *et al.* (1974), primarily because most observations were made from a distance, usually with the aid of binoculars. However, the parental behavior of brooding the very young (< 6 days) nestlings would probably compensate for any lack of the ability to shiver in these birds. Interestingly, Hudson

et al. (1974) show that shivering is not effective in Cattle Egrets until they are about 5 days old.

As the nestlings grew older, parental attentiveness less often took the form of brooding and more often consisted of standing one or two meters away from the nest. During this period the behavior of the nestlings played a major role in determining their thermal state. Young nestlings were capable of moving about in the nest. Because many nests had at least a partial exposure to the sun during parts of the day, the chicks could often move in and out of the sun by moving only a short distance. This situation is also seen, but somewhat more elaborately, in Roadrunners whose nests are apparently built to provide both sun and shade (Ohmart, 1973). During cool or windy periods when the adult was off the nest, the young herons would huddle together. This behavior was first noted in Cattle Egrets by Blaker (1969) and was observed by me more often in this species than in the other herons.

At high T_a when the adult was off the nest, the nestlings of all four species often responded behaviorally. The nestlings moved apart and spread out in a prone position, sometimes allowing their heads to hang outside the nest itself. This posturing probably increased their surface/volume ratio and thus increased convective heat loss. As the nestlings grew larger this prone posture gave way to the posture described above for adults as "shading:" back to sun, wings drooped. The most commonly observed response in nestlings to high T_a was gular fluttering. All four species show the capacity to gular flutter from hatching. This has been reported before for Cattle Egrets by Blaker (1969) and Hudson *et al.* (1974). Hudson *et al.* showed that young nestlings could dissipate

1.4-2.9 or more times their metabolic heat production by evaporative water loss at high T_a (44-45°C). Most of this evaporative water loss came from gular fluttering and panting, but some was presumed to come from excrement smeared on the abdomen of young nestlings before their plumage was fully developed. I have observed excrement on the abdomens of nestlings of all the heron species investigated. Whether or not high T_a stimulates excretion in the nest is speculative. However, one nestling Cattle Egret raised in the lab was capable of excreting outside the "nest" after about 10 days. Ricklefs and Hainsworth (1969) showed that Cactus Wrens nesting in the desert left more fecal sacs in the nest as T_a increased through the breeding season. This resulted in a lowering of nest temperatures; effects on nestling T_b were not discussed.

The interaction of nestling and parental behavior may often be complex and results, presumably, in the stabilizing of T_b at a high level in the nestlings. Two examples should illustrate these behaviors. Two neighboring Cattle Egret nests were observed July 3, 1974 between 1030 and 1200 hours. At the start of this period, the wind was moderate to brisk, and $T_a < 28°$ under a cloudy sky. The parent at nest CE-105 lay on two nestlings, aged 3 and 4 days, until about 1100 hours. At that time, the sun broke through, and the wind calmed. T_a in the sun was not determined at this time, but when the sun reappeared an hour later under similar conditions, $T_a = 36.0°C$. The parent then stood up and shaded its two nestlings. At 1120, clouds obscured the sun again, and the adult lay down on the nestling once again. In nest CE-106, there were four nestlings which included individuals older than the nestlings of CE-105. The parent of CE-106 was somewhat less attentive, so thermoregulation

became largely a function of nestling behavior. The four nestlings in CE-106 were 6, 5, 4, and 3 days; the youngest nestling was a runt. At 1030 hours, the parent was off the nest, and the young birds huddled together. At about 1055 the parent lay on the nestlings. Five minutes later the sun reappeared, and the parent arose, briefly shaded its chicks, then moved about 2 feet from the nest. By 1110, all of the young had spread out assuming a prone position; two, which could be clearly seen, gular fluttered. After the sun disappeared behind clouds at 1120, gular flutter stopped. By 1130, the wind had picked up again and the nestlings huddled together.

By the time heron nestlings are 9 or 10 days old, they are capable of leaving the nest to climb on adjacent branches. These "branchers" (Siegfried, 1966b) were first noted at 9 days old in Cattle Egrets by Blaker (1969). The ability to move out of the nest has great significance for the brancher in altering its thermal environment. By the time they were 12-13 days old, the branchers were so adroit at leaving the nest, they could rarely be caught.

The thermoregulatory effect of parental and then, increasingly, nestling behavior can be seen by looking at nestling body temperatures. Body temperatures of young birds were taken within 5 min of entering the heronry. The results are shown in Table 9. Of the young Louisiana Herons whose T_b was measured, three came from singleton nests, 10 from nests with twins, and 10 from nests with triplets. Of the Snowy Egret nestlings, one was a singleton, the other two were twins. Two of the Cattle Egret chicks in Table 9 were singletons, five were from nests with twins, and nine were from nests with triplets. Among the Little

Table 9. Body temperatures of young herons at the nest.

Species	T_b[a]	N_1[b]	N_2[c]	T_a Range[a]	Age Range[d]
Louisiana Heron	38.9 ± 0.3	23	19	20.5 - 36.4	0-9
Snowy Egret	38.9 ± 0.1	3	3	(31.5)	0-2
Cattle Egret	38.9 ± 0.2	16	16	26.0 - 32.6	1-14
Little Blue Heron	38.5 ± 0.6	7	5	27.0 - 35.0	0-5

[a]Measured in °C.

[b]Total measurements.

[c]Number of different individuals measured.

[d]Measured in days, where the first day of life is age 0.

Blue nestlings measured for body temperature, only one was a singleton and six were twins; no triplet nestlings were measured. No differences in T_b could be attributed to the number of young in the nest, T_a, or age in any species, as reflected by the small variance around each mean T_b. The very similar mean T_b among all the species is probably a consequence of their similar behavioral responses to the thermal environment even where the insolation varied greatly (see Chapter 3). The values of T_b reported in Table 9 are about 1°C below the 40°C reported for Cattle Egret nestlings by Hudson *et al.* (1974). Such a difference could easily be caused by the 5 min period of parental absence due to my disturbance.

The inability of young nestlings to maintain a high T_b in the absence of a parent was evident in the following cases. On May 9, 1974, a Cattle Egret nest (CE 4) in the shade (T_a = 30°C) had three nestlings, aged 6, 5, and 1 day old, all huddled together. T_b was 36.5°C, 36.0°C, and 33.0°C respectively. The parent had been scared away by my presence an undetermined period of time earlier (>> 5 min). On May 19, 1975, an adult Snowy Egret was flushed from its nest (SE 3). After 15 min, the T_b of its singleton nestling was 35.3°C. The nestling had hatched that day and weighed only about 18 g. The lower T_b of the smaller chicks in these two cases is related to their level of homeothermy as discussed below.

Development of Homeothermy

Dawson and Hudson (1970) and Dunn (1975) review an extensive literature on the development of homeothermy in birds. The only study of the development of homeothermy in ardeids has been by Hudson *et al.*

(1974) who investigated Cattle Egrets. Their study in fact demonstrated the development of endothermy in Cattle Egrets. That was not possible in this study since metabolism of nestlings was not measured. As a result, homeothermy cannot be linked conclusively to a given level of internal heat production but must instead be defined as the ability of young birds to maintain a T_b at least 75 percent of adult T_b at low T_a (*ca.* 20°C) for one or two hours (Dunn, 1975). This ability may be due to increased insulation because of emerging plumage, increased vasomotor control, reduced surface/volume ratio, better muscular coordination (*e.g.*, more effective shivering), a higher rate of metabolism, or a combination of some or all of these.

Figures 8-11 show nestling cooling curves at different ages for Louisiana Herons, Snowy Egrets, Cattle Egrets and Little Blue Herons respectively. The temperature differential ($T_b - T_a$) is plotted as its natural log against time. The resulting slopes are therefore the cooling constants (α) with units of min^{-1}. Generally, the older the nestling, the slower it cools. Therefore the cooling constants get progressively smaller with increasing age. At least brief periods of homeothermy are attained by 13 days.

Many of the curves for a given individual show two or more slopes. This is first seen in nestlings 8 or more days old but one Snowy Egret showed it at 6 days. A young heron is apparently capable of maintaining increasing ($T_b - T_a$) levels for short periods of time. After about an hour ($T_b - T_a$) drops at a rate reminiscent of younger nestlings. This is suggestive of a drop in metabolic activity. When the final cooling constants (*i.e.*, the only cooling constants in the younger nestlings)

Figure 8. Louisiana Heron cooling curves.

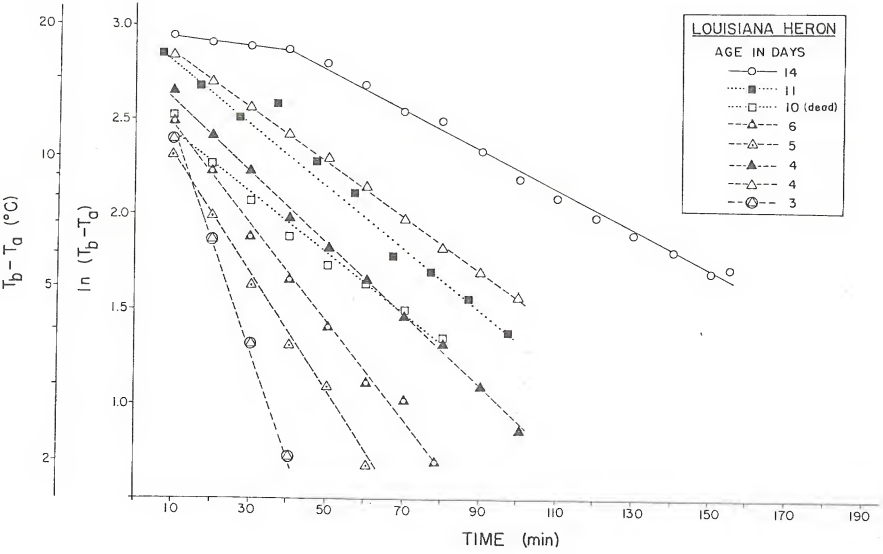

LOUISIANA HERON
AGE IN DAYS
14
11
10 (dead)
6
5
4
4
3
$T_b - T_a$ (°C)
ln $(T_b - T_a)$
TIME (min)
20
10
5
2
3.0
2.5
2.0
1.5
1.0
10
30
50
70
90
110
130
150
170
190

Figure 9. Snowy Egret cooling curves.

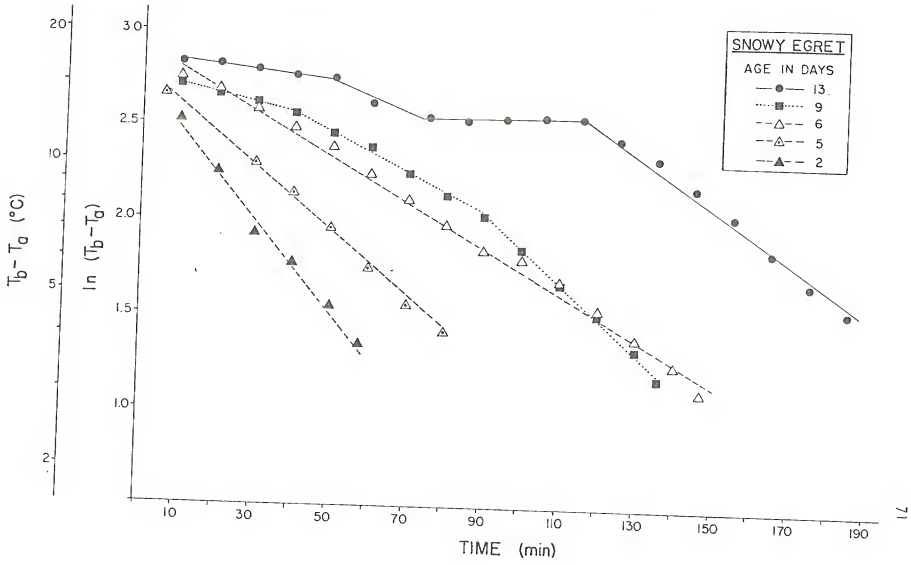

SNOWY EGRET
AGE IN DAYS
13
9
6
5
2
$T_b - T_a$ (°C)
ln $(T_b - T_a)$
TIME (min)
20
10
5
2
3.0
2.5
2.0
1.5
1.0
10
30
50
70
90
110
130
150
170
190

Figure 10. Cattle Egret cooling curves.

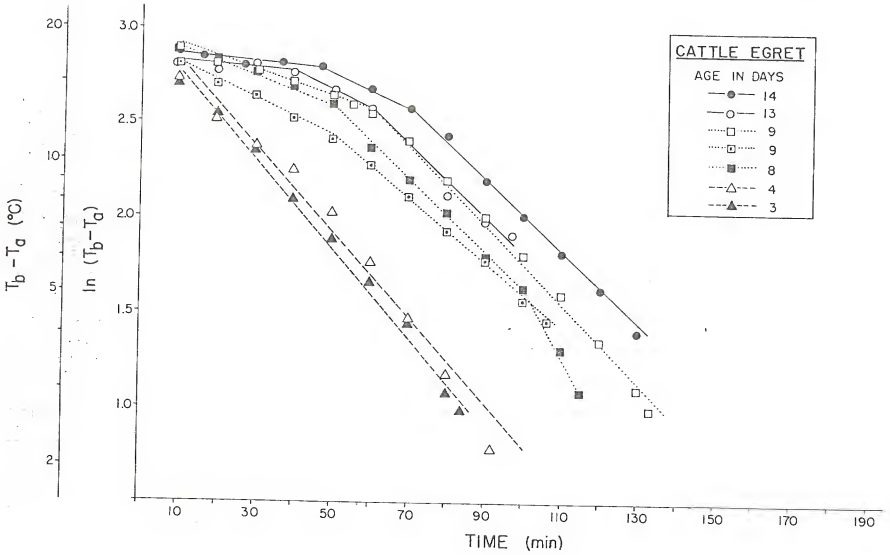
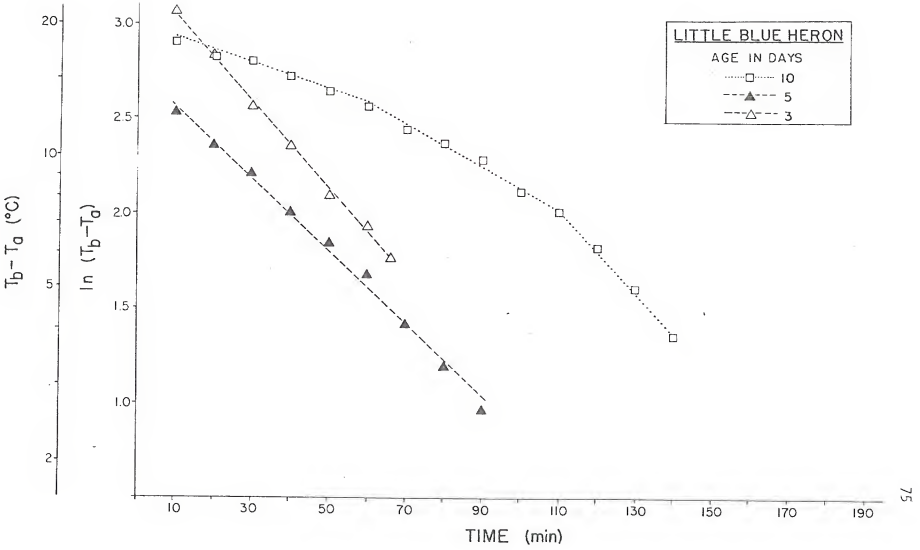

CATTLE EGRET
AGE IN DAYS
14
13
9
9
8
4
3
$T_b - T_a$ (°C)
ln $(T_b - T_a)$
TIME (min)
20
10
5
2
3.0
2.5
2.0
1.5
1.0
10
30
50
70
90
110
130
150
170
190

Figure 11. Little Blue Heron cooling curves.


LITTLE BLUE HERON
AGE IN DAYS
10
5
3
$T_b - T_a$ (°C)
ln $(T_b - T_a)$
TIME (min)
20
10
5
2
3.0
2.5
2.0
1.5
1.0
10
30
50
70
90
110
130
150
170
190

are compared for most species, they are remarkably similar, showing only a small decrease with age (see Table 10). This residual difference is probably due to a decreasing surface/volume ratio as well as emerging plumage. It is likely then that initial cooling constants in older nestlings reflect a considerable metabolic contribution.

The initial cooling constant is probably of greatest ecological significance. It represents the cooling a nestling would first undergo when left alone. Usually the change to a higher a does not occur for at least 40 min. By that time, these nestlings (nearly all branchers by this age) could change their thermal environment by, for example, moving into sunlight. Only on cool windy days in the absence of a parent would this time be exceeded before a suitable environment could be found. Ellis and Ross (in prep.) demonstrated that cooling constants could be used to predict the time a poikilotherm (here prehomeothermic birds) had before its T_b approached T_a:

$$t = \frac{ln(T_b - T_a)_t - ln(T_b - T_a)_i}{-a} \qquad (17)$$

where $(T_a - T_b)_i$ is the initial temperature differential.

The natural log of the initial cooling constant is plotted against age in Figure 12 to determine differences among the species. The correlation coefficients, r, for Snowy Egrets, Little Blue Herons, and Cattle Egrets are 0.99, 0.99, and 0.95 respectively, whereas r for Louisiana Herons is only 0.81. The slope (-0.173) for Louisiana Herons is the lowest, and although it is close to that of Little Blue Herons (-0.186), most of the Louisiana Heron data lie above their slope. The Lousiana Heron also showed the poorest level of homeothermy at the 13-14 day age class. This all tends to indicate that Louisiana

Table 10. Cooling constants[a] in nestling herons.

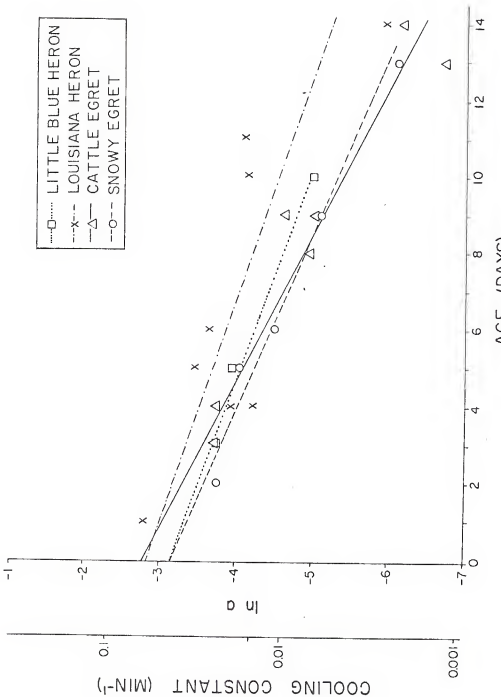
Species	Age	Period I	II	III
Louisiana Heron	2	59.57		
	4	14.52		
	4	19.07		
	5[b]	32.04		
	6	25.79		
	10[c]	16.12		
	11	16.52		
	14	2.66	10.79	
Snowy Egret	2	23.95		
	5[b]	17.20		
	6	11.20	13.15	
	9	5.12	10.67	17.80
	13	2.77	7.80/6.07	14.80
Cattle Egret	3	23.47		
	4	23.29		
	8	7.10	19.24	35.84
	9	9.75	17.58	
	9	6.48	21.30	
	13	1.20	9.40	18.18
	14	2.10	9.52	19.86
Little Blue Heron	3	23.11		
	5	19.38		
	10	6.58	10.98	21.87

[a]Taken from slopes of Figures 8-11; numbers in body of table are $x10^{-3}$.

[b]Raised in lab; body weight corresponds to 2-day-old chick.

[c]Dead.

Figure 12. Rates of homeothermic development in herons.


LITTLE BLUE HERON
LOUISIANA HERON
CATTLE EGRET
SNOWY EGRET
COOLING CONSTANT (MIN-1)
1.0
.100
.1000
ln a
-1
-2
-3
-4
-5
-6
-7
0
2
4
6
8
10
12
14
AGE (DAYS)

Herons achieve homeothermy more slowly than the other species. At present, the poor fit of the Louisiana Heron data to their slope cannot be explained. However, it results in such anomalies as the two 4-day-old chicks having a cooling constant comparable to an 11-day-old nestling.

Cattle Egrets show the fastest development of homeothermy, followed by Snowy Egrets. Their slopes from Figure 11 are -0.261 and -0.226 respectively. Hudson *et al.* (1974) indicate that endothermy is achieved in the 10-12 day-old class of Cattle Egrets.

Two nestlings were removed from their nests at 1 day and taken to the laboratory. One was a Louisiana Heron, the other a Snowy Egret. Growth was stunted in these birds so their weight at 5 days, when cooling curves were made, resembled that of nestlings only 2 days old. Nevertheless, the Snowy Egret showed a cooling constant in keeping with its age. The 5-day-old Louisiana Heron is difficult to evaluate due to the scatter of data in that age group.

The ability of a brood to become homeothermic before any individual in it could regulate has been reviewed by Dunn (1975). An extreme case was cited by Yarbrough (1970) where a brood of 4-5 Gray-crowned Rosy Finches (*Leucosticte tephrocotis griseonucha*) could regulate their temperature 6 days before any individual could. The huddling in herons as described above is probably a mechanism to allow collective homeothermy at relatively low T_a ($\leq$ 30°C) before the individual nestlings were able to thermoregulate. As might be expected, older nestlings (> 10 days) were not observed huddling. Unfortunately, cooling curves were not developed for nestling broods in this study. But McManus and Singer (1975) working with the Mongolian gerbil (*Meriones unguiculatus*)

demonstrated that thermal conductance fell as brood size increased. Huddling probably acts only in reducing heat loss by decreasing the effective surface/volume ratio.

Dunn (1975) in a review found that growth rate is the best predictor of the age of endothermy (although many of her sources provide age of homeothermy, not true endothermy). Growth in all four species of herons is given in Table 11. These values were converted to growth constants (K) using the method provided by Ricklefs (1967). The three *Egretta* species seem to fit the logistic equation best. The Cattle Egret shows a slowing of growth in the later ages measured, which is a characteristic of the Gompertz equation (Ricklefs, 1967). Nonetheless, the Cattle Egret fits the logistic equation slightly better. This is interesting because the Gray Heron (*Ardea cinerea*) and the Green Heron (*Butorides virescens*) fit the Gompertz equation (Ricklefs, 1968). The data provided in Table 11, especially for the Little Blue Heron and Snowy Egret, cover too small an age range to claim one equation with certainty. However, unless later growth is very different, all species do seem to fit only the logistic model. The asymptotic weight in the Ricklefs model could not be determined by strictly graphic methods, due to the lack of growth data for older nestlings. Instead an asymptote was selected to give the highest correlation coefficient (r) when age was plotted against the logistic conversion factors. The asymptotes are presented with the growth constants in Table 12. The Little Blue Heron (430 g) and Louisiana Heron (420 g) asymptotes probably do approximate the upper limits of adult weight. However, 530 g is certainly an overestimate for the Snowy Egret. Even so, if the Snowy Egret had had an

Table 11. Growth in nestling herons.[a, b]

Age	Louisiana Heron	Snowy Egret	Cattle Egret	Little Blue Heron
0	19.4 ± 0.4 (17)	21.5 ± 2.0 (2)	19.7 ± 0.7 (8)	22.0 ± 0.6 (3)
1	25.4 ± 0.6 (16)	26.5 (1)	25.5 ± 0.3 (11)	23.8 ± 1.2 (2)
2	35.3 ± 2.2 (6)	33.0 (1)	35.1 ± 1.7 (11)	30.0 (1)
3	44.2 ± 3.1 (6)	--	42.1 ± 3.8 (6)	39.0 (1)
4	60.0 ± 5.2 (9)	71.5 ±14.5 (2)	55.8 ± 1.8 (8)	--
5	77.7 ± 3.8 (9)	62.5 (1)	69.5 ± 2.8 (8)	78.8 ± 5.7 (2)
6	--	126.5 (1)	81.6 ± 4.3 (4)	
7	--		109.1 ± 15.4 (4)	
8	--		--	
9	173.0 (1)		135.5 ± 7.4 (3)	
10	211.5 (1)		151.5 (1)	
11			182.0 (1)	
12			206.0 (1)	
13			178.2 ± 7.2 (2)	
14			181.0 (1)	

[a] Mean ± s.e., measured in g.

[b] Number in parentheses is sample size.

asymptote of 420 g, K would increase only 3 percent from 0.312 to 0.322. The asymptote for the Cattle Egret is certainly an underestimate of adult weight in the field. Hudson *et al.* (1974) equated their asymptote with fledging weight, but I see no *a priori* reason for doing this. The asymptotic weights for Cattle Egrets measured in Florida in this study agree with those provided by Hudson *et al.* for Texas and South Africa (based on data from Siegfried, 1972).

Table 12 also shows the rates of development of homeothermy (H) which are the slopes from Figure 12. Cattle Egrets in Florida (and Texas) grow more slowly than the other species, and develop homeothermy more rapidly. But this inverse relationship does not seem to hold among the other herons. Over a wider range of species, Dunn (1975) found that a positive relationship existed between growth rate and the development of homeothermy.

Color in Nestling Herons

In very small, essentially ectothermic chicks, heat loss is a major problem. As the bird grows, its surface/volume ratio decreases, its metabolic rate increases, and its insulative plumage increases. At a certain point, heat loss is no longer the main problem, but rather heat gain becomes of primary concern. At this stage, metabolic heat production may be too high, surface/volume ratio too small, and insulation too great to withstand long periods of solar radiation. Usually all of these problems are controlled by parental or nestling behavior. But occasionally, behavior will not suffice.

One way of coping with heat loss for short periods is solar brooding. This has been reported for Roadrunners (Ohmart, 1973) and

Table 12. Comparative growth in herons using the logistic equation.[a]

Species	Location	Asymptote[b]	K[c]	H[d]	Source
Louisiana Heron	Florida	420	0.301	-0.173	Present study.
Little Blue Heron	Florida	430	0.288	-0.186	Present study.
Snowy Egret	Florida	530	0.312	-0.226	Present study.
Cattle Egret	Florida	290	0.248	-0.261	Present study.
Cattle Egret	Texas	270	0.232	--	Hudson *et al.*, 1974
Cattle Egret	South Africa	300	0.326	--	Hudson *et al*,. 1974 (based on data from Siegfried, 1972).

[a]From Ricklefs, 1967.

[b]Estimated asymptotic weight in g.

[c]Growth constant.

[d]Rate of homeothermic development in days^{-1}.

suggested for Piñon Jays (Balda and Bateman, 1972; Bateman and Balda, 1973). Roadrunners, Piñon Jays and the herons studied here all have very dark skin. The down on the herons is initially too sparse to cover all the skin. The nature of the plumage of Little Blue Herons and Louisiana Herons is illustrated by McVaugh (1973). Hudson *et al.* (1974) and especially Weber (1975) provide photographic evidence of exposed skin in Cattle Egret nestlings of various ages.

To illustrate how important solar brooding might be, two examples of heat loss will be given. For consistency, both examples utilize Cattle Egrets; the cooling constants are taken from Figure 11. Equation (10) relates the time it takes to cool to the cooling constant. Assume T_a = 28.9°C in both examples, and that preferred T_b = 38.9°C (see Table 9). Equation (17) can be rearranged so that:

$$\ln(T_b - T_a)_t = \ln(T_b - T_a)_i - at \quad \text{but,}$$

$$\ln(T_b - T_a)_t = \ln(38.9°C - 28.9°C) = 2.303 \quad \text{so,}$$

$$\ln(T_b - T_a)_t = 2.303 - a \cdot t \quad \text{and}$$

$$(T_b - T_a)_t = e^{(2.303 - a \cdot t)} \quad \text{therefore}$$

$$(T_b)_t = (T_a)_t + e^{(2.303 - a \cdot t)} \qquad (18)$$

In the first example, a new hatchling (0 days old) is exposed to T_a = 28.9°C for 10 min while its parent stands up to turn any other eggs in the nest, chase an intruder, or attempt to feed an older sibling. The cooling constant for the hatchling is 0.0627. Then from equation (18) after only 10 min, T_b has dropped to 34.2°C. In the second example, a 6-day-old chick which still has dark skin showing between feather tracts, is the youngest of three nestlings; its oldest sibling is 10 days. The

parent has left the nest for an hour. Even at T_a = 28.9°C, the older two siblings do not huddle. From Figure 11, the cooling constant of the youngest bird is 0.0129. After 60 min, T_b will have dropped to 33.5°C.

The absorption of solar radiation in both the examples above could prevent the large drop of T_b. This is probably a function of the dark skin. It is interesting that the small pink-skinned chick of White Ibises hatches out completely covered in dense black down. Bartholomew and Dawson (1954) indicated that down may protect young birds, including Great Blue Herons (*Ardea heroidas*), from solar radiation. Although that must certainly be true once internal heat production is relatively high and the surface/volume ratio is relatively low, very young chicks may face problems of heat loss rather than heat gain.

Linsdale (1936:117) reported a correlation of nestling plumage (especially down) with insolation. Looking at 15 Great Basin icterids and fringillids, he noted that "birds which nest in exposed situations and which live in hot regions have pale or pallid nestling plumages and nest linings which reflect" solar radiation.

The reason why dark Little Blue Herons have young with white plumage whereas dark Louisiana Herons have young with dark plumage has to do with nesting patterns and the transition from a problem of heat loss to one of heat gain. If adults leave their young unattended once the oldest nestling is about 12.6 days old, younger siblings will not yet be homeothermic. Even the older siblings will not be totally independent of their thermal environment. But the younger siblings will not be capable of leaving the nest very readily. If left alone under high solar intensity at high T_a, the chicks might not survive. Their white

plumage (see Figure 1 for Little Blue Heron fledgling) helps protect them by reflecting much of the solar radiation. The Louisiana Heron generally nests in the shade. Presumably nesting in the sun would require more parental attention to keep their older dark nestlings from overheating. One Louisiana Heron nest was found in the sun in 1974. The adults continued attentive behavior (mostly shading one nestling) for 23 days. This is longer than observed for any other nest of any of the four species. Such intense parental care must necessarily reduce the amount of food gathering possible and so lower the number of young fledged from the nest.

CHAPTER 6

THE SIGNIFICANCE OF COLOR IN HERONS

The color of birds that nest colonially or feed in open areas has been discussed at least since Darwin (1896). Darwin (1896: 493) noted that sea birds have a white plumage more often than terrestrial birds. He suggested that these birds would be conspicuous in a white or black plumage; conspicuous coloration would aid the birds in locating one another for mating. Yapp (*fide* Siegfried, 1971a) has pointed out that the communal roosts of birds are conspicuous. Craik (1944) contended that sea birds were white, or had white undersides, to reduce their contrast to the sky while in flight, enhancing their ability to surprise prey items in the ocean. However, Armstrong (1944) noted the large number of dark birds that dive for food, and Cowan (1971) refuted Craik experimentally.

The debate on color in these birds is epitomized by the controversy over color in herons, especially polymorphism in herons. Several herons are dimorphic: the Reef Herons (*Egretta sacra* and *E. gularis*), the Little Egret (*E. garzetta*), the Reddish Egret (*Egretta* [= *Dichromanassa*] *rufescens*) have white and dark morphs; even the Least Bittern has a rare melanistic phase (Meyerriecks, 1960). Two of the best known dimorphic herons occur in North America. The Great Blue Heron (*Ardea herodias*) has a white morph which is often given subspecific status (*A. h. occidentalis*) and apparently represents a

Caribbean population. *Ardea herodias* appears to be the only dimorphic heron for which a genetic mechanism has been suggested (Mayr, 1956). The Little Blue Heron's dimorphism is unique in the Ardeidae because the white morph is the juvenile of the species. Darwin (1896: 494) incorrectly suggested this sort of dimorphism in a reef heron.

Meyerriecks (1960) reviewed the arguments of several authors who believe color in herons is related to feeding habits. Murton (1971) is the most recent advocate of this view. He said that white or dark color are cryptic colors, white color being more common in herons that feed in open waters during the day, and dark color facilitating hunting in more closed areas. He also noted that dark herons tend to be more active hunters. Murton suggested that white juvenal plumage in Little Blue Herons is useful for feeding on insects in grassland areas as Cattle Egrets do. Meyerriecks (1960) and Recher (1972) discounted color as an aid to feeding by pointing out the lack of behavioral differences between light and dark morphs of a species when feeding. This extends to the juvenile and adult Little Blue Herons which show no differences in manner of prey capture except that the juvenile is less efficient (Recher, 1969).

Murton (1971) postulated that polymorphism has evolved in herons occupying coastal habitats in the absence of closely related species "which might otherwise partition the resources." This may be possible, but not for the reasons Murton suggested. He believed that different colored morphs would exploit different food resources in the habitat; but the lack of differences in the feeding ecology and behavior of different morphs of a species belie this. However, apostatic selection,

(as discussed by Johnson and Brush, 1972) which promotes polymorphism in predators by reducing the ability of prey to generalize a single search image of a predator, could be occurring. This hypothesis would probably be easily tested experimentally.

Meyerriecks (1960) considered white color in herons to be conspicuous in order to facilitate social interactions. He noted that the most social herons are white. Recher (1972) stated that the white juvenal plumage of Little Blue Herons may be related to their post-breeding dispersal and the tendency of juveniles to feed in flocks at this time.

Recher (1972) noted a correlation between color polymorphism, coastal (actually, open) environments, and tropical latitude. It is true that most polymorphism in herons is confined to low latitudes. Recher stated that in hot exposed environments, "white-coloured herons. . . may be better able to regulate their body temperatures than their dark siblings" while feeding. Very few workers have looked to see whether white herons even normally hunt in direct sunlight during the heat of the day. Siegfried (1971b) found that feeding activity in Cattle Egrets is reduced during that part of the day. However, I have shown that white plumage certainly confers a degree of protection from insolation among nesting Cattle Egrets and Snowy Egrets and nestling Little Blue Herons. Meyerriecks (1960) rejected the notion that white color is useful in temperature regulation, because he has seen Little Blue Herons and Green Herons remain in the sun for hours. The basal metabolism of Green Herons is not known, but M_b for Little Blue Herons

is sufficiently low (see Chapter 4) that they are able to stay in the sun in spite of their color.

The various theories on color polymorphism in herons fall into four main classes: 1) Herons are conspicuously white in order to facilitate social interactions; 2) light and dark phases are cryptic to facilitate feeding; 3) light and dark phases are the result of apostatic selection which facilitates hunting by deemphasizing a search image that prey can use; 4) white color confers thermal stability in a hot environment. Of these, 2) is least likely, although it may operate for a few species. Experimentation is needed to test 3), but the lack of polymorphism at high latitudes raises a question about apostatic selection. Neither 1) nor 4) can be easily dismissed. Unfortunately 1) cannot be tested; 4) can be tested because it is a function of characteristics (*e.g.*, reflectance and rate of metabolism) which can be measured. Although juvenal plumage in Little Blue Herons may enhance social interactions, it seems to be primarily a thermal adaptation (see Chapter 5). Whether white coloration in Snowy Egrets and Cattle Egrets is primarily for social facilitation, thermal stability, some other factor or some combination of these cannot be known with certainty. However, white plumage does contribute to the ability of these birds to nest in a hot sunny environment. The selective force(s) responsible for dark coloration in Louisiana Herons and adult Little Blue Herons is even more obscure. Nevertheless, as a consequence of their dark color, these birds can only live in a hot environment by having special behavioral or physiological adaptations.

CHAPTER 7

CONCLUSIONS

Louisiana Herons, Snowy Egrets, Cattle Egrets, and Little Blue Herons nest together in a hot environment with high insolation. Cattle Egrets and Snowy Egrets are able to nest in the sun because 1) their white plumage reflects most of the incident solar radiation in the visible spectrum and about half of the near infrared radiation below 900 μm; and 2) they have a basal metabolism (M_b) only 85 percent of that expected from their weight. The two dark herons reflect very little of the solar radiation to which they are exposed. In addition, Louisiana Herons also have a slightly higher M_b than expected (107 percent); their nesting strategy is to build nests in the shade. The Little Blue Heron, however, does not preferentially select nest sites in the shade. Instead, it shows a host of adaptations which allow it to nest successfully in sites exposed to the sun. The M_b of Little Blue Herons is only 66 percent of that expected from their weight, a relationship shown for other dark birds in a hot environment as well. They are less attentive in incubating than white Cattle Egrets when their nests are in the sun at similar ambient temperature (T_a), although attentiveness is about the same for the two species in the shade. Unlike Louisiana Herons, Little Blue Heron young have a white plumage which probably is of value in preventing overheating in the sun in the absence of a parent and before complete homeothermy has developed. Egg

temperature for all species is about 35°C. Paradoxically, all four herons hatch with heavily pigmented skin which continues to show at the apteria for over a week. This pigmentation is considered an adaptation for solar brooding when the nestlings are so small that heat loss is a greater problem than heat gain.

All four species show the same general form of behavioral thermoregulation at the nest. Parents brood small nestlings for most of the first week. At high T_a, they may shade their young which are all capable of evaporative heat loss by gular flutter from their first day. As the nestlings age, their parents spend progressively less time on the nest, and temperature regulation increasingly depends upon their own behavior. At cool T_a, small nestlings huddle, whereas at high T_a, they spread apart and lie prone in their nest. By the time the parents begin spending long periods of time away from the nest, the chicks are old enough to leave the nest and change their thermal environment. The effectiveness of the complex of parental and nestling behaviors is seen in that body temperature = 38.9°C in nestlings of all species regardless of T_a, age, or brood size.

Cooling curves show that short term homeothermy is gradually achieved by 12-13 days in all four species. Cattle Egret nestlings appear to develop homeothermy fastest, Louisiana Herons slowest. Growth in all four species tentatively can be considered to conform to the logistic equation, although the slow Cattle Egret growth at later nestling ages makes this species nearly fit the Gompertz equation.

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Hugh Irl Ellis was born May 29, 1944 in Burbank, California. He attended school in Southern California and began college at the University of California at Berkeley in 1962. He received his A.B. in Zoology from there in 1967. Subsequently he was enrolled at California State University at Northridge (then San Fernando Valley State College), where he received an M.S. in Biology, from 1967 to 1970. In 1970, Mr. Ellis enrolled in graduate school at the University of Florida in pursuit of a Ph.D. in Zoology, which is to be awarded in June, 1976. His main fields of research interest are physiological and behavioral ecology. In 1974 Mr. Ellis was named Teacher-of-the-Year by the Graduate School. In 1975 he received a Chapman Memorial Fund grant to help support his research. Mr. Ellis is a member of the Ecological Society of America, the American Association for the Advancement of Science and the American Ornithologists' Union.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

John H. Kaufmann, Chairman
Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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